Fishery Bulletin

Vol. 84, No. 1 January 1986

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Fishery Bulletin

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Southeast Fisheries Center Miami Laboratory
National Marine Fisheries Service, NOAA
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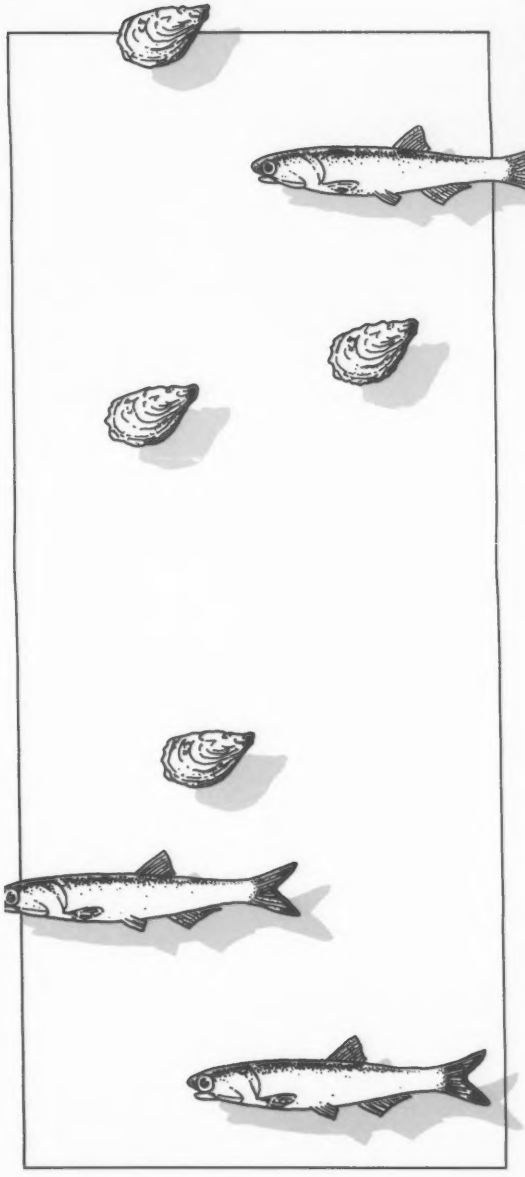

Best NMFS Publications for

83

The Publications Advisory Committee of the National Marine Fisheries Service has announced the best publications authored by the NMFS scientists and published in the *Fishery Bulletin* and the *Marine Fisheries Review* for 1983. Only effective and interpretive articles which significantly contribute to the understanding and knowledge of NMFS mission-related studies are eligible, and the following papers were judged as the best in meeting this requirement:

"Seasonal variation in survival of larval northern anchovy, *Engraulis mordax*, estimated from the age distribution of juveniles" by Richard D. Methot, Jr. appears in *Fishery Bulletin* 81:741-750. Richard D. Methot, Jr., fishery biologist is from the Southwest Fisheries Center's La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, California 92038.

"To increase oyster production in the northeastern United States" by Clyde L. MacKenzie, Jr. appears in *Marine Fisheries Review* 45(3):1-22. Clyde L. Mackenzie, Jr., fishery biologist is from the Northeast Fisheries Center's Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, New Jersey 07732.

AWARDS

STARVATION-INDUCED MORTALITY OF YOUNG SEA-CAUGHT JACK MACKEREL, *TRACHURUS SYMMETRICUS*, DETERMINED WITH HISTOLOGICAL AND MORPHOLOGICAL METHODS

GAIL H. THEILACKER[1]

ABSTRACT

Young jack mackerel, *Trachurus symmetricus*, living offshore are starving while those living nearshore are healthy. These results for sea-caught jack mackerel were determined by using histological and morphological criteria that reliably diagnosed the viability of laboratory-raised jack mackerel. Both the histological and morphological indices indicated that 350 km offshore about 70% of the first-feeding jack mackerel were starving. In contrast, 12% of the fish collected near islands and banks were starving. In both habitats, mortality rates decreased to zero for jack mackerel at 2 weeks of age. The accuracy of the techniques for prediction of the nutritional state of wild larvae is discussed and evaluated.

Jack mackerel, *Trachurus symmetricus*, hatch with yolk reserves that last for 5 d at 15°-15.5°C. After the yolk is absorbed, they must eat within 3 d or die of starvation. In addition, growth is retarded in larvae that have experienced only 1 d of starvation, and resumption of normal growth does not occur until 2-3 d after the starvation period (Theilacker 1978, 1981). Thus, in the laboratory, availability of food at the time of first feeding affects growth and survival of young jack mackerel. In the field, the relative importance of starvation as a source of mortality of jack mackerel is unknown. It was first suggested by Hjort (1914) (reviewed by May 1974) that the strength of the year class is determined early in life by the availability of food for larvae at the time of first feeding (the critical period hypothesis). But only recently (O'Connell 1980) has the presence of starving ocean-caught larvae been documented. In this study I give evidence that starvation may be a major cause of natural mortality of young jack mackerel at sea. I use two techniques, developed in the laboratory, to determine the incidence of starvation (Theilacker 1978). The potential use of these techniques to monitor sea samples for larval survival is discussed.

METHODS

Collection

In May 1980 a concentration of jack mackerel eggs and larvae was located 350 km off the coast of California (lat. 31°00'N and long. 120°30'W). A 400 mi^2 grid was established which contained 41 stations, 4 mi apart; it took 4 d to sample all stations (Fig. 1). At each station, a standard oblique bongo net tow (Smith and Richardson 1977) and a 1 m net sample were taken. The bongo samples will be used in another study to estimate growth and mortality of jack mackerel larvae (Hewitt et al. in press). The 1 m net (505 μm mesh) was used to sample larvae qualitatively from the upper 50 m of water. Ahlstrom (1959) found that 88% of the larval jack mackerel collected off California were in the upper 50 m, and all the jack mackerel collected by Devonald (1983) were above 42 m. A special collection procedure was used for the samples taken for histological and morphological analyses. Immediately after the net tow, the sample was preserved in Bouin's solution to avoid autolysis of larval tissues (elapsed time was usually 8 min) (Theilacker 1978). The collecting net was not washed down (a procedure required for quantitative samples), and the cod end containing the sample was placed directly into Bouin's solution. The preserved sample was removed from the cod end within an hour. After 2 d, Bouin's solution was replaced by 70% alcohol.

In addition to jack mackerel collections taken in the open ocean 350 km offshore, a few special tows (n = 24) for assessment of starvation were made during routine cruises in 1978, 1979, and 1980 near the Channel Islands (Anacapa, Santa Barbara, and San Clemente) and Tanner Bank.

Preparation of Fish

More than 2,000 jack mackerel were collected in

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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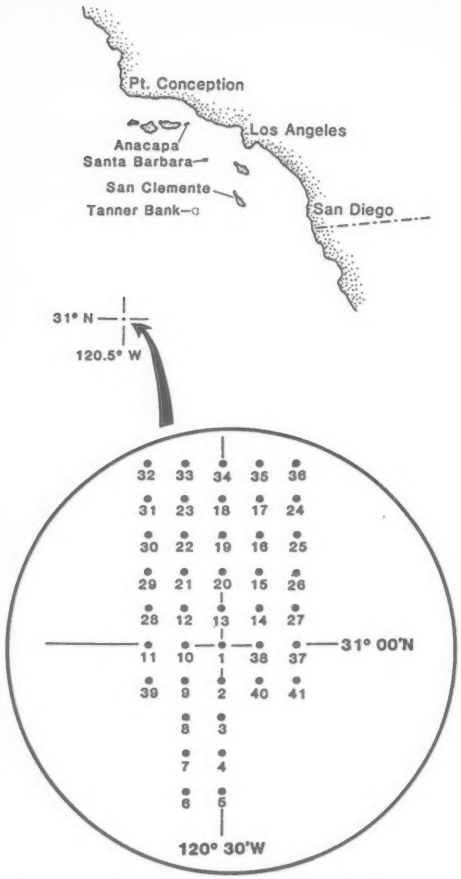


FIGURE 1.—Location of jack mackerel, *Trachurus symmetricus*, collections off the coast of California. Nearshore stations were at Anacapa, Santa Barbara, and San Clemente Islands and at Tanner Bank. The grid of open-ocean stations was 350 km offshore; stations were 4 mi apart.

samples taken offshore; from 0 to 262 fish were caught per sample (Table 1). Larvae sorted from the samples (n = 445) were counted and five body measurements taken: standard length (SL, tip of upper jaw to perpendicular at end of notochord); head length (HL, tip of upper jaw to cleithrum); eye diameter (ED); body depth at the pectoral (BD-1); and body depth at the anus (BD-2). After measurement, some larvae (n = 369) were prepared for histological examination. When samples contained fewer than 50 jack mackerel, most larvae were examined, but when samples contained more than 100 jack mackerel, about 25% of the fish were examined histologically. Jack mackerel size distribution in the offshore study area (determined for 400 fish taken from stations 16, 23, 34, and 35) was similar among stations and ranged between 2.6 and 4.7 mm SL. To ensure analysis of all ages in the larger samples, fish were taken equally from each of four length classes: <3.0; 3.0–<3.5; 3.5–<4.0; 4.0–<5.0 mm. These larvae were imbedded in paraffin, sectioned at 6 μm, and stained with Harris hematoxylin and eosinphloxine B (Theilacker 1978). In my analysis of histological data I combined the first two size classes because the size at first feeding was 3.2 mm.

The prevalence of starvation was assessed for 371 jack mackerel selected from 20 of the 32 positive stations (Table 1). In addition, I analyzed 41 jack mackerel taken in 14 hauls from the inshore stations near the Channel Islands and Tanner Bank.

Histological Analysis

The histological assessment of nutritional state is based on distinct cellular changes that occur in tissues when larval jack mackerel were deprived of food; these changes are well documented by Umeda and Ochiai (1975), O'Connell (1976), and Theilacker (1978). To determine the condition of individual ocean-caught jack mackerel, I used the histological criteria I developed in the laboratory by starving jack mackerel except I did not grade the pancreas. Grades were assigned to 11 histological characteristics of the brain, digestive tract, liver, and musculature (Theilacker 1978, 1981). Fish identities were unknown during this examination. I classified jack mackerel larvae into four categories (healthy, recovering, starving, and dying) according to their histological scores (the summation of the grades for each of the 11 histological characteristics).

Tissues of jack mackerel from the sea which had tissues similar in appearance to the tissues of feeding, laboratory-raised fish were classified as healthy; sea-caught jack mackerel which resembled laboratory fish that had fasted before eating were classified as recovering (these fish showed signs of feeding and digestion, but also showed signs of starvation); sea-caught larvae which were classified as starving resembled larvae that had been starved in the laboratory for 1-3 d (Theilacker 1978, 1981). I did not observe the dying category in laboratory-starved larvae; this category is described in Results.

Morphological Analysis

To detect starvation I used a set of morphological

TABLE 1.—Number of jack mackerel collected and the condition of those that were analyzed histologically.

Station No.	Number of fish					
	Sampled	Analyzed	Dying	Starving	Recovering	Healthy
Offshore						
1	0	0				
2	2	1	0	0	1	0
3	0	0				
4	2	0				
5	0	0				
6	0	0				
7	2	1	0	1	0	0
8	2	2	0	0	2	0
9	1	1	1	0	0	0
10	0	0				
11	3	3	3	0	0	0
12	0	0				
13	1	0				
14	1	0				
15	>200	0				
16	>200	0				
17	20	13	0	8	5	0
18	>125	0				
19	43	35	7	0	1	27
20	242	64	8	19	13	24
21	>250	0				
22	>175	0				
23	150	32	1	0	4	27
24	1	0				
25	23	0				
26	4	3	3	0	0	0
27	0	0				
28	262	58	3	36	14	5
29	11	11	1	4	4	2
30	250	57	4	13	18	22
31	32	9	7	1	0	1
32	109	25	0	2	20	3
33	31	23	1	3	10	9
34	38	0				
35	43	0				
36	31	24	3	4	1	16
37	7	5	2	1	2	0
38	2	2	1	0	0	1
39	0	0				
40	1	0				
41	0	0				
Total (Offshore)	>2,264	369	45	92	95	137
Around Islands						
Anacapa	12	12	0	1	0	11
Santa Barbara	3	3	0	0	2	1
San Clemente	17	17	0	1	5	11
Tanner Bank	9	9	0	1	0	8
Total (Nearshore)	41	41	0	3	7	31

characteristics that successfully diagnosed the extent of starvation in 85% of the laboratory-reared jack mackerel (Theilacker 1978). The technique is based on a stepwise discriminant analysis (SWDA) using 11 body part measurements. The analysis allowed me to distinguish between individuals belonging to fed and starved treatments, given a set of morphological measurements that describe the characteristics of the individuals in each feeding treatment. The 11 body part measurements used to distinguish between groups of fed and starved jack mackerel were 1) head length, 2) eye diameter, 3) body depth at the pectoral, 4) body depth at the anus, 5) head length/standard length, 6) eye diameter/standard length, 7) body depth at the pectoral/standard length, 8) body depth at the anus/standard length, 9) eye diameter/head length, 10) body depth at pectoral/head length, and 11) body depth at anus/head length. Standard length was used in the ratios but not as a unit to allow discrimination between feeding and starving fish of the same length.

Adjustment for Shrinkage

In order to use morphological measurements to diagnose starvation of jack mackerel, it is essential to adjust for shrinkage of body measurements. Both handling and preservation cause shrinkage of larval fishes, and the amount of shrinkage varies among body parts. Final fish size is dependent not only on initial size but also on the handling time (which is different for the laboratory and the field) and the type of preservative used (Blaxter 1971; Theilacker 1980a; Hay 1981). The shrinkage of laboratory specimens of jack mackerel preserved in Bouin's solution is known (Theilacker 1980a), but for field-collected specimens the shrinkage caused by the net tow and the subsequent effect of Bouin's preservative must be evaluated.

I conducted laboratory experiments to estimate the amount of shrinkage caused by handling (net retention) and by preservation. Live jack mackerel were pipetted individually (time = 0) onto a slide, and four body measurements were taken before placing the fish into a net container through which 15°C seawater circulated. Standard length, head length, eye diameter, and body depth at the anus were measured. Body depth at the pectoral fin was not measured because it was difficult to measure quickly on live jack mackerel. During net treatments, I usually remeasured each fish four more times at 5-7 min intervals, replacing the fish in the net between each set of measurements. After 25-30 min, the fish were preserved in either Bouin's fixative (used for histological analyses) or 5% buffered Formalin[2] (as per shipboard procedures; Smith and Richardson 1977). Remeasurements after preservation were taken in 3-4 wk.

Shrinkage of net-captured larval fish has been shown to decrease with increasing fish size. For example, shrinkage of northern anchovy decreased from 19% at 4 mm SL to 8% at 18 mm SL (Theilacker 1980a). The jack mackerel tested in this study ranged between 3.35 and 4.10 mm SL, and within this restricted length group shrinkage was proportional to size. Thus for the shrinkage analyses, all jack mackerel were combined into one group.

For the combined size group, length of the jack mackerel body (Fig. 2) and the head continued to shrink for the duration of the net treatment. Width of the body (Fig. 3) and the eye shrank initially, and then remained relatively constant during additional treatment. To account for positive correlation between body parts, a multivariate analysis (Table 2) was used to relate the ratio of net-treated size to live size (for each body part) with treatment time. Individual shrinkage was highly variable; for example, shrinkage of body depth varied between 0 and 23% for treatment times between 5 and 20 min (Fig. 3). However, since these were the best estimates of average shrinkage for body parts, the regressions (Table 2) were used to calculate the adjustment factors needed for this study. Factors for each body part

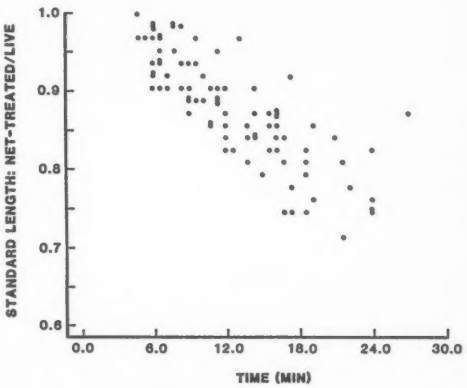


FIGURE 2.—Shrinkage of standard length, shown as the ratio of net-treated size to live size, of individual *Trachurus symmetricus* larvae as a function of net-treatment time; estimated parameters are in Table 4.

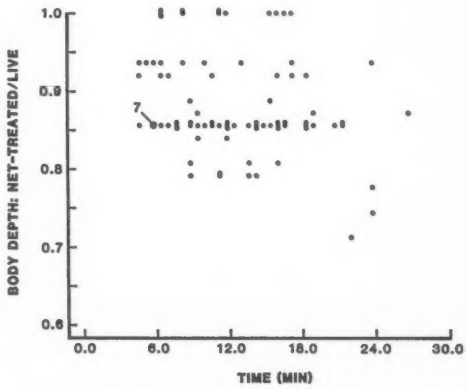


FIGURE 3.—Shrinkage of body depth, shown as the ratio of net-treated size to live size, of individual *Trachurus symmetricus* larvae as a function of net-treatment time; estimated parameters are in Table 4.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Shrinkage of jack mackerel larvae. Parameters estimated from multivariate linear equations relating the ratio of the net-treated size of a mackerel body part to its live size (y) with the net-treatment time (x).

Net-treated size/ live size[1]	a	(SE)	b	(SE)	P[2]	r^2
Standard length (SL)	1.0109	(0.0117)	−0.0105	(0.0008)	<0.001	0.66
Head length (HL)	0.9281	(0.0157)	−0.0038	(0.0011)	0.001	0.12
Eye diameter (ED)	0.9360	(0.0168)	−0.0027	(0.0012)	0.031	0.06
Body depth (BD-2)	0.8980	(0.0177)	−0.0014	(0.0013)	0.280	0.02

[1]n = 89.
[2]Probability that slopes differ from zero.

were calculated by 1) combining the shrinkage ratio at 8 min (average elapsed time for field collections, see Methods) with 2) the average shrinkage in Bouin's preservative after the net treatment, and 3) comparing the combined shrinkage with results from shrinkage determined in the laboratory study (Theilacker 1980a; Table 3). Also given in Table 3 are average shrinkage ratios calculated for specified time intervals.

Adjustment factors for standard length, head length, and eye diameter (Table 3) support the view that shrinkage of field-collected fishes is greater than shrinkage of fishes preserved in the laboratory. Shrinkage of BD-2 was an exception to this pattern, however, as less shrinkage occurred under simulated field conditions (20-23%) than in the laboratory (25%). I (Theilacker 1980a) reported a similar paradox for northern anchovy where simulated-field net treatments caused 8% shrinkage of BD-2 as compared with 10% shrinkage for standard laboratory preservation. Jack mackerel shrinkage was greater in Bouin's solution than in Formalin, results which are consistent with studies on northern anchovy. Also, as with northern anchovy, Formalin preservation caused a slight increase in the size of the jack mackerel eye (Table 3).

I adjusted the body measurements of the ocean-caught jack mackerel with the shrinkage factors (ratio R_8, Table 3). Use of these adjustments should equate the morphology of preserved, ocean-caught jack mackerel (this study) with the morphology of preserved, laboratory-raised jack mackerel that were used to develop the morphological SWDA (see Methods: Morphological Analysis). It was necessary to reestimate the SWDA function for this study, although nearly the same analysis was made previously (Theilacker 1978). A new estimate was required because pectoral body depth was not included in the shrinkage measurements in this study; hence, an SWDA function that excluded this measurement was needed. Elimination of pectoral body depth from the analysis reduced the level of predictability from 85% to 78%. This new function was used here to classify the condition of ocean-caught jack mackerel

TABLE 3.—Shrinkage of jack mackerel larvae[1]. Treatment ratio (R) is treated size divided by previous size (1.00 = no shrinkage).

Treatment ratio	R	n	Ratios: Mean time	Standard length	Head length	Eye diameter	Body depth
8 min net/live size	[2]R_1	89	8	0.93	0.90	0.91	0.89
5-10 min net/live size	R_2	36	7.3	0.94	0.90	0.92	0.89
11-15 min net/live size	R_3	22	12.6	0.87	0.88	0.88	0.86
16-28 min net/live size	R_4	27	19.4	0.81	0.86	0.89	0.88
Bouin's fixative/ net-treated size	[3]R_5	15	—	0.91	0.84	0.93	0.91
Formalin fixative/ net-treated size	[3]R_6	13	—	0.96	0.93	1.08	0.91
Laboratory-preserved in Bouin's fixative live size	[4]R_7	45	—	0.92	0.82	0.90	0.75
Calibration factor = $R_7/R_1 \times R_5$	[5]R_8	—	—	1.09	1.08	1.06	0.93

[1]Range in standard length 3.35-4.10 mm.
[2]Calculated from regression (Table 2); ocean-caught fish preserved within 8 min; see text.
[3]Shrinkage in fixative after net treatment.
[4]Data from Theilacker (1980a).
[5]Adjustment factor to equate measurements of field-collected mackerel (this study) with measurements of laboratory-raised mackerel (Theilacker 1978).

after the size of their body parts was adjusted for shrinkage.

RESULTS

Habitat Conditions

A larval-density gradient was apparent in the open ocean study area. High densities of jack mackerel larvae (100-<300/sample) were found in the central stations and in stations near the western boundary of the grid; lower densities (20-50) were found to the north and east, and densities of larvae approached zero at the southern stations that were occupied at the beginning and again at the end of the 4-d observation period (Fig. 4). Larval densities in the south did not change during this period.

The study area was chosen because temperature, viewed on satellite thermal image of the sea surface, corresponded to the temperature range (15°-16°C) associated with jack mackerel spawning (Farris 1961). Surface temperature in the study area increased from 15.2°C in the north to 16.8°C at the southern stations, with the majority of jack mackerel found in water temperatures of 16.1°-16.6°C. Water temperatures inshore of the grid were about 14°C.

A temperature-salinity curve obtained at station 19 (Fig. 1) agreed well with the curves obtained from inshore stations with the exception of the warm-water portion of the curve, which appeared to be a thin, warm lens of open ocean water intruding coastward over deeper coastal water.

Histological Assessment of Fish Condition

I used the tissue characteristics of laboratory fish (raised at 15.0°-15.5°C) of known feeding history as the criteria to determine the nutritional condition of the sea-caught jack mackerel. Photomicrographs of the diagnostic tissue characteristics were documented by Theilacker (1978). Many of these characteristics are shown also for wild fish (Fig. 5, see also Figures 6-14). In addition, the wild fish exhibited four tissue conditions that were not observed in the laboratory: lesions in the brain; luminal vacuoles in the midgut; total degeneration of the midgut mucosal cells; and a wavy configuration of the muscle fibers. Each of these conditions will be considered in the following section that describes the tissues of ocean-caught fish. My emphasis will be on those tissue characteristics that diagnose starvation in young jack mackerel.

Brain

The brain of an ocean-caught jack mackerel was considered normal when the neurons were distinct, round, and closely spaced. In these fish, brain cell division was common, but it was not graded. One percent of the jack mackerel examined had brain lesions of the type (Fig. 6) induced by ultraviolet light in larval northern anchovy, *Engraulis mordax*, and Pacific mackerel, *Scomber japonicus* (Hunter et al. 1979). The grading system classified these jack mackerel (n = 3) into the healthy category. In a

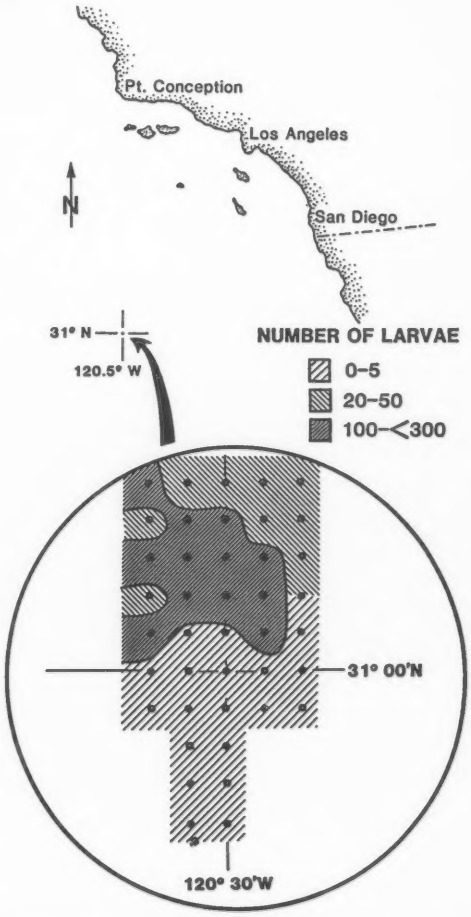


FIGURE 4.—*Trachurus symmetricus* larval density gradient shown as number of larvae collected per sample (not quantitative). Station grid located 350 km off the coast of California.

single specimen, lesions were present not only in the brain but throughout the spinal cord (Fig. 7) as well. In addition, the gut and associated glands had deteriorated to the extent that this fish was considered starving.

An abnormal central nervous system of a jack mackerel larva consisted of vacuolar degeneration and shrinkage of neurons. The degenerating neurons exhibited increased staining (Fig. 8).

Digestive Track and Associated Glands

The midgut mucosa of young jack mackerel is composed of a single layer of columnar epithelial cells. Older fish (3.7-4.0 mm) showed increased mitotic activity in the basal layer. Microvilli bordered the midgut lumen only in fish that appeared healthy. Mucosal cells were closely united in the fish considered to be normal (Figs. 9, 10). Basal separations between these cells were common, not only in fish that appeared to be starving but also in fish that showed signs of feeding and digestion (Fig. 11). O'Connell (1980) also reported that sea-caught northern anchovy exhibited basal separations between mucosal cells while the apical portions were well joined.

All wild jack mackerel categorized as recovering had basal separations between midgut mucosal cells. Laboratory fish that were artificially starved for 1-2 d before feeding showed these separations for several days after feeding resumed. In the laboratory, larvae did not grow while their tissues were regenerating (Theilacker 1981).

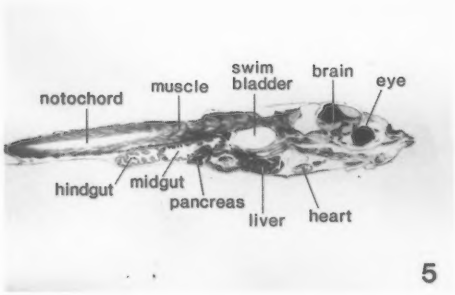
Many sea-caught jack mackerel of all ages had intracytoplasmic vacuoles in the midgut epithelium. Basal and membrane lined, these vacuoles resembled the vacuolar condition found in some recovering, laboratory fish (Theilacker 1981). In addition, many sea-caught larvae had smaller, luminal vacuoles that were found in the laboratory fish (Fig. 12). These luminal vacuoles may indicate a degenerative condition. In higher vertebrates a metabolic imbalance can cause vacuolar degeneration. Vacuolation appears first as numerous small, clear vacuoles dispersed throughout the cytoplasm. As the condition becomes more severe, these minute vacuoles coalesce to form large (sometimes single) clear spaces that displace the nucleus (Anderson 1971). On the other hand, the numerous luminal vacuoles can secrete mucous into the lumen or store fat. Use of a routine mucicarmine staining was negative for the presence of mucous cells. Unfortunately, the presence of fat in the vacuoles could not be tested because fat is removed during tissue preparation by clearing agents. Neither vacuolar condition was graded.

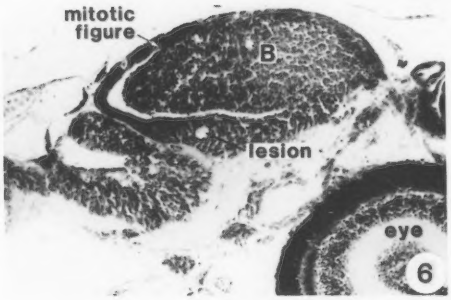
Another unusual condition of the midgut occurred in many of the smaller wild jack mackerel. In these fish, the margin of the lumen had lost its integrity, microvilli were absent, and the sloughing of the mucosal cells into the lumen (a condition common in starved laboratory jack mackerel) appeared to have progressed until the lumen contained masses of undefinable, cellular material (Fig. 13). O'Connell (1980) described a comparable condition which he found in the midgut of a single, northern anchovy specimen, the smallest examined. All jack mackerel exhibiting this condition were smaller than the size attained at first feeding, indicating shrinkage had occurred. The hindgut also contained necrotic debris, and other diagnostic tissues were in poor condition. These jack mackerel were classified as dying.

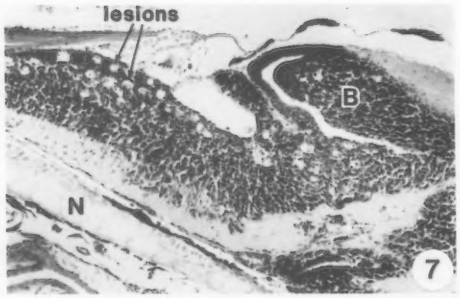
Hindgut mucosal cells of wild jack mackerel typically showed eosin-staining inclusions that are reported to be sites of intracellular digestion (Iwai 1968, 1969; Iwai and Tanaka 1968; Watanabe 1981). Inclusions in the wild jack mackerel varied in intensity; in healthy specimens the intensity appeared to be related to time of day (feeding period), increasing during daylight hours and decreasing during the night. Although the presence and intensity of hindgut inclusions were noted, they were not graded. Inclusions were not present in larval teleosts deprived of food in the laboratory (Theilacker 1978; Umeda and Ochiai 1975; O'Connell 1976). However, in many wild jack mackerel showing signs of starvation the presence of pale inclusions indicated that the fish had eaten at some time in the past.

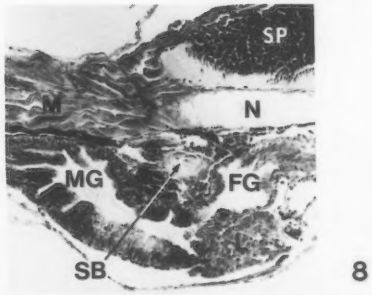
The key diagnostic characteristics of the pancreas were obscure in ocean-caught jack mackerel because of the intensity of staining. In laboratory fish, the pancreas was very sensitive to food deprivation. For example, a breakdown in the symmetry of the acinar secretory unit was detectable after 1 d of food deprivation (Theilacker 1978). In the wild fish, the intensity of the staining of the pancreas was difficult to control (see Fig. 12), and I was not able to obtain consistent results, hence the condition of the pancreas was not evaluated.

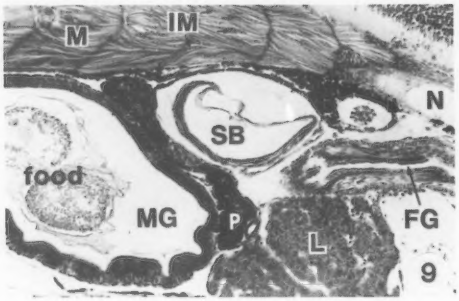
The jack mackerel liver was considered normal when hepatocytes had clear, distinct nuclei (Fig. 9). The appearance of the cytoplasm was quite variable; in some larvae very few intracellular spaces existed in the cytoplasm of the hepatocytes whereas in others extensive intracellular spaces existed. Presumably these spaces are areas where glycogen and fat are stored within the cell. This presumed incorporation of stores was most marked in healthy











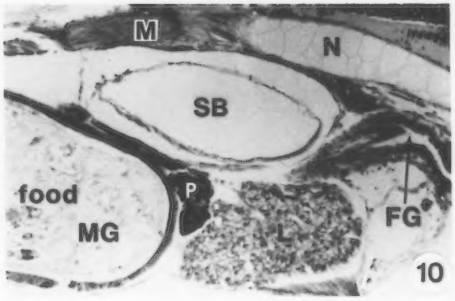


FIGURE 5.—*Trachurus symmetricus* larva, 3.75 mm SL. All 11 histological criteria graded as healthy. Bar = 281 μm.

FIGURE 6.—Head of *Trachurus symmetricus* larva graded healthy. Mitotic activity and the location of brain lesions are indicated. Bar = 47 μm. B = brain.

FIGURE 7.—*Trachurus symmetricus* larva graded as starving. Lesions present throughout brain and spinal cord. Bar = 47 μm. B = brain, N = notochord.

FIGURE 8.—Pectoral area of a dying *Trachurus symmetricus* larva showing darkly stained primitive nerve cells, wavy muscle fibers, necrotic and atrophied liver, and loss of integrity of midgut mucosal cells. Bar = 47 μm. FG = foregut, L = liver, m = muscle, MG = midgut, N = notochord, SB = swim bladder, SP = spinal cord.

FIGURE 9.—Pectoral area of healthy *Trachurus symmetricus* larva collected offshore showing parallel muscle fibers and abundant intermuscular tissue, distinct nuclei in liver and midgut, and good cellular integrity. Note deflating swim bladder. Bar = 47 μm. FG = foregut, IM = intermuscular tissue, L = liver, M = muscle, MG = midgut, N = notochord, P = pancreas, SB = swim bladder.

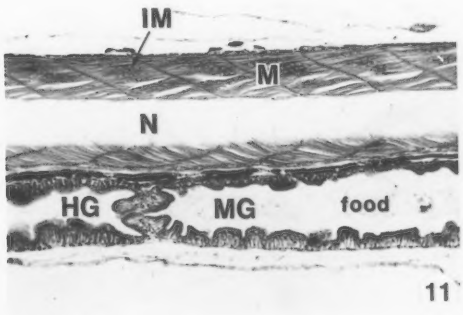
FIGURE 10.—Pectoral area of healthy *Trachurus symmetricus* larva collected near San Clemente Island showing abundant glycogen reserves in the liver. Bar = 47 μm. FG = foregut, L = liver, M = muscle, MG = midgut, N = notochord, P = pancreas, SB = swim bladder.

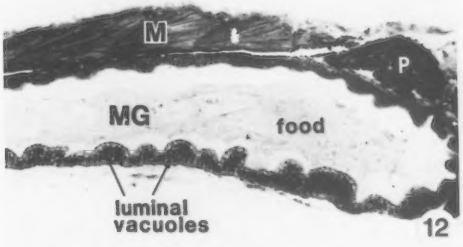
jack mackerel collected near islands and banks (Fig. 10) whereas healthy jack mackerel collected offshore showed moderate to little storage (Fig. 9).

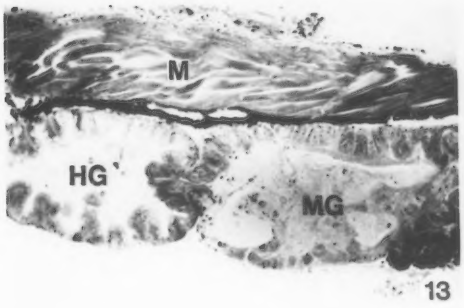
At the other end of the grading scale, the shrunken livers of jack mackerel considered to be starving contained darkly stained hepatocytes composed of evenly stained cytoplasm with indistinct, irregular nuclei.

Musculature

Healthy muscle tissue in jack mackerel had the following characteristics: few spaces between the muscle fibers; distinct and parallel, striated myofibrils; and abundant, basophilic and nucleated intramuscular tissue (Fig. 9). Nourishment was considered inadequate in fish exhibiting separated (Figs. 11, 14) and hyaline muscle fibers (Fig. 13) and a reduction (Figs. 11, 14) or absence (Fig. 13) of intramuscular tissue. In some sea-caught jack mackerel, muscle fibers were wavy (Fig. 8). Presence of wavy muscle fibers in wild fish was considered abnormal because it was always associated with the poor condition in the other diagnostic tissues, but this characteristic was not used in classification. In starved laboratory fish, nonparallel fibers were reported (Theilacker 1978, 1981), but the wavy pattern was unusual. There were fish with intermediate spaces between muscle fibers that, according to the scores of the other diagnostic tissues, appeared healthy. The







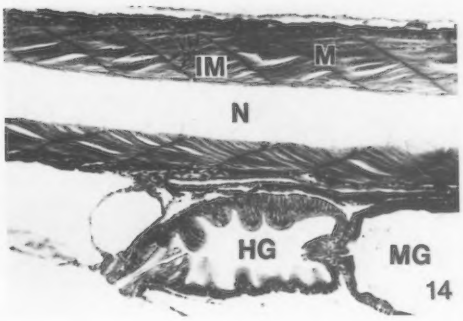


FIGURE 11.—*Trachurus symmetricus* larva graded recovering. Prominent separations between midgut and hindgut epithelial cells, slight muscle fiber separation and intermediate intermuscular tissue containing distinct nuclei. Bar = 47 μm. HG = hindgut, IM = intermuscular tissue, M = muscle, MG = midgut, N = notochord.

FIGURE 12.—Healthy *Trachurus symmetricus* larva showing luminal vacuoles in the midgut. This histological characteristic was not graded. Bar = 47 μm. M = muscle, MG = midgut.

FIGURE 13.—*Trachurus symmetricus* larva graded dying. No intermuscular tissue; hyaline muscle fibers; total degeneration of midgut mucosa. Bar = 34 μm. HG = hindgut, M = muscle, MG = midgut.

FIGURE 14.—Recovering *Trachurus symmetricus* larva showing slight muscle fiber separation and slight reduction of intermuscular tissue. Bar = 47 μm. HG = hindgut, IM = intermuscular tissue, M = muscle, MG = midgut, N = notochord.

grading system usually classified these fish into the recovering category.

General Histological Observations

In jack mackerel that were considered healthy, swim bladder inflation was first noted at 3.4 mm. Swim bladders were inflated in larvae taken at night whereas they were deflated in those taken in the day. The swim bladders of 72% of the fish were deflated by 0700 (n = 81) except for fish scored in the starving category where inflation was common at any time of day, which was possibly a symptom of starvation or an additional energy-sparing function of the swim bladder (Hunter and Sanchez 1976).

Theilacker (1978) pointed out that the gallbladder was always enlarged in jack mackerel that were deprived of food in the laboratory, and this condition occurred in sea samples of starved larvae taken in the day. On the other hand, gallbladder enlargement was also found in the healthy fish as well as starved fish collected at night. According to Love (1970), the gallbladder discharges its contents when stimulated by food. Jack mackerel do not eat at night, so the gallbladder of healthy fish may remain distended during the night. Thus enlargement of the gallbladder was not used to diagnose starvation. Theilacker's (1978) samples of fed and unfed fish were taken only during the day, when feeding occurs.

Mitotic figures in the brain of jack mackerel occurred in fish collected at all times of day and night. On the other hand, mitosis of mucosal cells in the midgut was restricted to the night. It seems that mucosal cells of northern anchovy also divide late at night, when the digestive tracts are empty (O'Connell 1981).

Evidence for Starvation in the Sea

Results of the histological analysis showed that starvation was a major source of mortality for the smallest jack mackerel larvae (<3.5 mm) as 59% appeared to be dying of starvation, 23% were eating but had fasted previously, and only 19% were classed as healthy. The incidence of starving larvae decreased to 16% in the 3.5-4.0 mm size class and was 3% in the older larvae (Table 4). The numbers of fish used for the histological assessment of starvation was adequate for the smallest (<3.5 mm SL) larval size class (coefficient of variation ranged between 0.09 and 0.15 for the four condition categories), but larger samples would be needed to give a reliable estimate of the fraction starving for the older larvae (>3.5 mm SL) because of the low incidence of starvation.

Despite the fact that jack mackerel abundance decreased from west to east and north to south (Fig. 4), I found no consistent differences in the incidence of starvation between fish taken from areas of high larval density and those taken from areas of low larval density (Fig. 15). Therefore, to estimate mortality due to starvation, I combined all samples collected in the offshore area. To estimate mortality rates on a daily basis, the observed number of fish belong-

TABLE 4.—Histological condition of jack mackerel collected 350 km off the coast of California.

	Dying	Starving	Recovering	Healthy	Total	Daily percent Starving[1]	Daily percent Dying[2]
Yolk sac	—	—	—	15	15	0	0
<3.5 mm							
Number	43	74	45	38	200		
Duration (d)	1	3	2	6			
Number/d	43	24.7	22.5	6.3	96.5	70	45
3.5-<4.0 mm							
Number	2	16	38	54	110		
Duration (d)	1	3	2	3.3			
Number/d	2	5.3	19	16.4	42.7	17	5
4.0-<4.5 mm							
Number	0	2	12	45	59		
Duration (d)	—	3	2	3.3			
Number/d	—	0.7	6	13.6	20.3	3	0

[1] $\frac{\text{Number dying/d + starving/d}}{\text{Total}}$

[2] $\frac{\text{Number dying/d}}{\text{Total}}$

ing to each size and health category was divided by the duration—the number of days jack mackerel are expected to remain in each category (Table 4). Durations spanned 1 to 6 d depending on age and condition. For healthy fish, duration is simply the size-class interval divided by the growth rate. Healthy fish belonging to the smallest size group (<3.5 mm) grow at 0.05 mm/d (Theilacker 1978) and begin to eat at 3.2 mm SL. Thus duration for this size interval (0.3 mm) was 6 d. Growth rate for older fish was 0.15 mm/d; the rate was determined for this study by counting daily growth increments in otoliths (Hewitt et al. in press). The duration that a larva remains in one of the starvation states is a function of the persistence of the histological criteria. Young jack mackerel deprived of food in the laboratory show signs of starvation for 3 d before dying, and larvae recovering from a period of starvation show these signs for 2 d (Theilacker 1978, 1981). Older fish may be more resistant to starvation, but as I had no information for older jack mackerel, I used the durations for younger larvae.

For the smallest jack mackerel living 350 km offshore, 45% were dying of starvation per day. Daily mortality dropped rapidly to 5% to zero for older larvae (Table 4). Increasing the durations for the older larvae in the starving and recovering categories (Table 4) decreases this estimate of daily mortality.

Results of the histological examination of jack mackerel collected near islands and banks allow a preliminary assessment of the effects of different habitats on starvation (Table 5; Fig. 16). A large difference existed in the daily larval mortality caused by starvation between the open ocean and island and bank habitats. In areas near the islands, none of the first-feeding larvae were dying of starvation whereas 45% from the open ocean were dying of starvation. In addition, healthy larvae taken near islands were apparently more fit than healthy larvae captured in the open ocean, as the larvae from the island habitats had abundant quantities of glycogen in the liver (Fig. 10), whereas livers of larvae from the open ocean rarely contained glycogen stores (Fig. 9). This indicates that food must have been much more abundant in the island habitat because not only were fewer fish starving but the healthy fish were able to store glycogen. The healthy fish from the open sea may have been just able to meet their daily metabolic requirements.

The morphological data gave essentially the same results as did the histological method. On the basis of morphometric evidence, 70% of the first-feeding jack mackerel (<3.5 mm SL) were starving and the number decreased to zero for older jack mackerel (Table 6). Although the results were similar, the morphological categories used to classify the fish were different from the histological ones. In particular, there was no morphological category for dying fish. For the morphometric SWDA, larvae were grouped by feeding treatment (Table 6), and the histological categories (Table 4) were based on the dominant larval tissue conditions determined to characterize a nutritional state. Thus the morphometric SWDA cannot be used to estimate the number of larvae dying per day due to starvation.

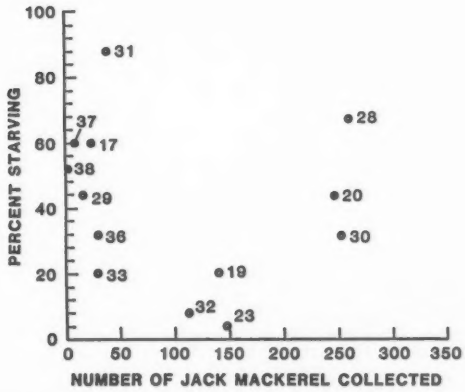


FIGURE 15.—Percentage of starving *Trachurus symmetricus* larvae (number starving/number analyzed) related to the number of larvae collected at each offshore station; station number is indicated.

DISCUSSION

Larval Starvation and Recruitment

Both histological and morphological criteria indicate that starvation is probably a major source of larval jack mackerel mortality at the time of first-feeding but that the survivors of this 6-d period are much less vulnerable to starvation. Prey (mainly young stages of copepods) are more abundant at the nearshore islands and banks off the coast of California than offshore (Beers and Stewart 1967, 1970; Arthur 1976, 1977; Devonald 1983), and survival of first-feeding jack mackerel was higher in the nearshore habitats than offshore. Thus selection of spawning sites may have a great effect on survival. Eggs and larvae of jack mackerel are very widely distributed; they occur from Baja California to British Columbia and up to 400 mi off the coast of

TABLE 5.—Histological condition of jack mackerel collected near islands and banks off the coast of California.

	Dying	Starving	Recovering	Healthy	Total	Daily percent Starving[1]	Daily percent Dying[2]
Yolk sac	—	—	—	—	0		
<3.5 mm							
Number	0	2	6	12	20		
Duration (d)	1	3	2	6			
Number/d	—	0.7	3	2	5.7	12	0
3.5-<4.0 mm							
Number	0	1	1	12	14		
Duration (d)	1	3	2	3.3			
Number/d	—	0.3	0.5	3.6	4.4	7	0
4.0-<4.5 mm							
Number	0	0	0	7	7		
Duration (d)	1	3	2	3.3			
Number/d	—	—	—	2	2	0	0

[1]$\frac{\text{Number dying/d + starving/d}}{\text{Total}}$

[2]$\frac{\text{Number dying/d}}{\text{Total}}$

TABLE 6.—Predicted condition of field-collected jack mackerel larvae determined with the morphometric technique.

	Starved 3 days	Starved 1 & 2 days	Fed	Total	Daily percent Starving[1]
<3.5 mm					
Number	48	66	150	264	
Duration (d)	[2]2	2	6		
Number/d	24	33	25	82	70
3.5-<4.0 mm					
Number	0	1	121	122	
Duration (d)	2	2	3.3		
Number/d	—	0.5	36.7	37.2	1.3
4.0-<4.5 mm					
Number	0	0	59	59	
Duration (d)	2	2	3.3		
Number/d	—	—	17.9	17.9	0

[1]$\frac{\text{Number starved/d}}{\text{Total}}$

[2]Unfed jack mackerel larvae die in 4 d.

California and up to 1,000 mi off Oregon and Washington (reviewed by MacCall and Stauffer 1983). In addition, jack mackerel have a protracted spawning season which extends from March through September. The bank and island habitat must be a very small fraction of the total spawning habitat; thus despite the higher survival in inshore areas, the offshore zone may be the most important. In addition, better feeding conditions around islands may be offset by a greater abundance of predators. Whether the large concentration of starving larval jack mackerel found offshore was an isolated case or a general condition in offshore areas is unknown.

Given that relative recruitment strength of jack mackerel year classes varies greatly and is rarely "average" (Fig. 17; MacCall and Stauffer 1983), the daily mortality rate of about 45% found in this study is not unrealistic. Considering the relatively long lifetime (i.e., 30+ yr) and high fecundity of jack mackerel, one can deduce that the overall mortality may be very high. This study certainly indicates that starvation at the onset of feeding may be an important factor influencing recruitment variation in jack mackerel.

O'Connell's (1980) study of northern anchovy is the only other study in which starvation in the sea has

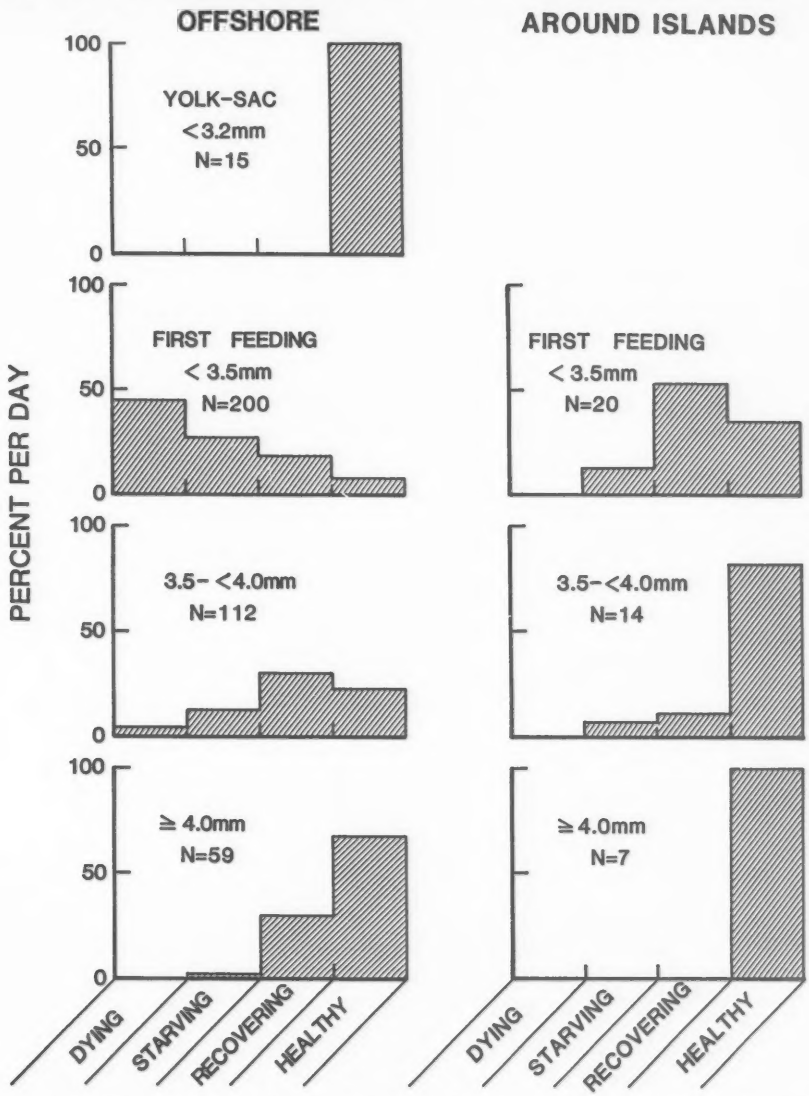


FIGURE 16.—Comparison of the nutritional condition of young *Trachurus symmetricus* collected from offshore and nearshore habitats. Daily percents taken from Tables 2 and 3.

been assessed using histological criteria. O'Connell examined 318 northern anchovy larvae from 64 stations that extended over a large area, 20-350 km off the coast of California. To compare the mortality of northern anchovy with the daily rates I found for jack mackerel, I calculated size-specific daily mortality of northern anchovy by using 1) O'Connell's (1980) histological evaluation, 2) information on time to irreversible starvation to determine durations (Lasker et al. 1970; Hunter 1981; Theilacker and Dorsey 1981), 3) information on shrinkage of ocean-caught northern anchovy to determine size at first

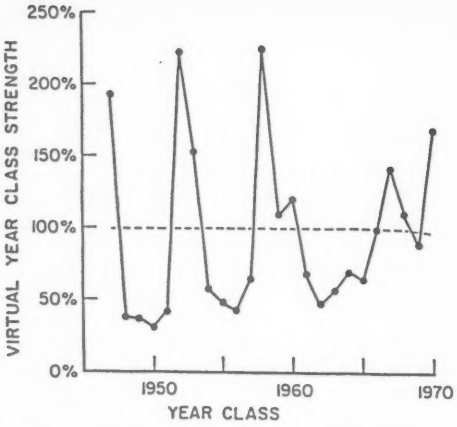


FIGURE 17.—Relative recruitment strengths of jack mackerel year classes in southern California. Virtual year-class strength is measured by the sum of percentage contributions to seasonal landings over the lifetime of the year class. The dashed line indicates average strength (from MacCall and Stauffer 1983; Fig. 4).

feeding (Theilacker 1980a), and 4) a growth rate of 0.37 mm/d for healthy sea-caught northern anchovy (Methot and Kramer 1979). Although the number of first-feeding larvae was low in O'Connell's data (n = 23), I calculated a starvation-induced mortality rate of between 35 and 46%/d. Thus my calculations indicate that substantial numbers of northern anchovy larvae as well as jack mackerel larvae are dying at the time of first feeding. This loss rate for northern anchovy is similar to estimated total mortality rate at this stage, 39%/d (Lo in press; 1978 data), which suggests that starvation is the major source of mortality at first feeding. This conclusion for northern anchovy could not be drawn at the time that O'Connell did his work because the data on net shrinkage were not known. The average rates estimated by O'Connell were much lower because he combined larval size classes.

Attempts to assess larval starvation in the sea using morphological criteria are more common (Shelbourne 1957; Honjo et al. 1959; Nakai et al. 1969; reviewed by May 1974; Ehrlich et al. 1976), but they have seldom been successful, probably because of the biases introduced by failure to correct adequately for shrinkage (see next section). Recently Devonald (1983) used a morphometric index with shrinkage adjustments to assess jack mackerel feeding regimes off California. She found good correspondence between jack mackerel condition and prey availability and concluded that feeding conditions were better near islands than in the area between islands. Several of her samples and my samples were taken concurrently (San Clemente and Tanner Bank; Table 1), and I found that 92% of the jack mackerel from the island habitat were healthy. Thus, my results obtained using histological criteria confirm Devonald's conclusion.

Other techniques used in the past to assess food availability include RNA/DNA (Buckley 1980), food in gut (Rojas de Mendiola 1974; Ciechomski and Weiss 1974; Arthur 1976; Ellertsen et al. 1981), and otoliths. Of course otolith work is critical because estimates of growth rates are essential for assessment of mortality, but it is of no value for assessing growth at the onset of feeding (Methot 1981).

Arthur (1976) conducted the only other study on the feeding of jack mackerel off the coast of California. He found, after examining the stomach contents of 750 specimens from 65 offshore samples, that 60% of the first-feeding jack mackerel and 10% of the older larvae (7 mm) had empty stomachs. This observation lends additional credence to my histological evaluation of jack mackerel collected offshore that shows 59% of the first-feeding fish and 3% of the older fish (>4 mm) were starving.

I believe my estimates of jack mackerel mortality due to starvation are conservative. The assumptions I made about the persistence of starvation and the duration of growth were based on extensive laboratory studies (Theilacker 1978, 1981). Because the majority of jack mackerel were collected at sites warmer (16.1°-16.6°C) than the culture temperature (15°-15.5°C), the durations for growth and starvation may be altered, but the final estimate of mortality due to starvation is higher after the appropriate changes to the durations are made. Furthermore, if net retention of robust fish is greater than retention of thin fish of the same length, starvation may be underestimated. In addition, the selection of unhealthy larvae by predators would also increase the starvation estimate.

Previous evidence supporting the occurrence of starving fish larvae in the ocean has been mainly circumstantial (reviewed by May 1974; Jones and Hall 1974; Lasker 1975). Evidence from this study and O'Connell's (1980) study shows that starvation does occur and that the young stages of jack mackerel and northern anchovy are highly vulnerable.

Comparison of Morphological and Histological Criteria for Starvation Diagnosis

The incidence of starvation based on mor-

phological criteria was essentially the same as that based on histological criteria. Owing to the relative ease, and low cost of measuring fish compared with a histological examination, the morphological analysis is an attractive approach. On the other hand, histological analysis defines a cause and effect relation between structure and starvation whereas gross morphological measurements provide an index of starvation which is highly vulnerable to errors and biases in calibration and interpretations. Because of the importance of these measurements in recruitment studies, it is appropriate to consider the merits of and potential errors in these techniques in some detail.

The morphometric approach relies on measurements of fish to compare reared and wild animals at the same developmental stage. Thus shrinkage adjustments are needed to intercalibrate laboratory measurements and field measurements. Fish shrink when collected in a net and preserved, and shrinkage of the size of all body parts is dependent on the time in the net, size of fish, and type of preservative used (Blaxter 1971; Theilacker 1980a; Hay 1981). In this study, tow time was controlled at 5 min and samples were preserved within 8 min. Thus damage to the fish and shrinkage were minimal, but the samples were not quantitative. It is doubtful that the morphometric technique will work with jack mackerel taken in standard, quantitative collections. Quantitative net tows are 20 min, and they include an additional hosing down of the nets before sample preservation (Smith and Richardson 1977). The procedure damages the larvae, causing extensive shrinkage which makes accurate measuring difficult. Further, a long tow time decreases confidence in time-specific shrinkage estimates because fish can be collected at any time during the towing period. Increasing the tow time also causes both the magnitude of the shrinkage correction factor and the standard error of its estimate to increase. For example, in this study, standard length of jack mackerel shrank by an average of 6.0 $\pm$ 0.6% in 8 min and 19.0 $\pm$ 1.0% in 20 min.

While laboratory calibration is absolutely essential for the morphometric analysis, no shrinkage calibration is needed for the histological analysis, and it might be possible to use the histological observations on other fishes. Diagnostic criteria for the starving condition of jack mackerel (Theilacker 1978), northern anchovy (O'Connell 1976), and yellowtail, *Seriola quinqueradiata*, (Umida and Ochiai 1975) were similar. In addition, important biological information is gained while using the histological approach whereas gross morphological indices provide no such information. For example, histological analysis of jack mackerel has revealed a pattern of diel swim bladder inflation and a disruption of this rhythm, accumulation of glycogen reserves, and brain lesions presumably produced by UV radiation (Hunter et al. 1979). There is just no substitute for this extensive biological information. On the other hand, population work requires large samples, and morphological indices are probably the only practical means for working with very large samples. Thus, the optimal experimental design for population work on starvation is probably the use of morphological criteria (calibrated for shrinkage) combined with a smaller subsample of fish which are graded histologically. All work requires special net tows, preservation, procedures, and laboratory calibration.

Caution needs to be exercised when transferring information obtained in the laboratory to the field. Raising larval jack mackerel in small containers is known to affect growth, nutritive condition, and possibly activity (Theilacker 1980b). Additionally, there is evidence that wild fish tend to be thinner than their laboratory counterparts (larval herring, Blaxter 1971; juvenile herring, Balbontin et al. 1973; larval northern anchovy, Arthur 1976). My use of the morphometric SWDA assumes that the morphometric criteria I developed in the laboratory for larval jack mackerel raised in large tanks are applicable to ocean-caught jack mackerel.

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Many thanks to Brian Rothschild who suggested research on the nutritive condition of larval fish and to William T. (Tosh) Yasutake who offered me a personalized course in teleost histology. The offshore collections were made possible by Roger Hewitt's effective planning, the crew of the RV *David Starr Jordan*, and the assistance of Jack Metoyer and Carol Kimbrell. Miguel Carrillo sorted the mackerel, Richard Kiy measured them, and Jack Metoyer prepared them for histological analyses. Metoyer also helped with the shrinkage study. Nancy Lo assisted with all statistical applications. I appreciate John Hunter's and Martin Newman's constructive reviews of the manuscript. Many thanks to the Technical Support Group for typing services.

LITERATURE CITED

AHLSTROM, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Wildl. Serv., Fish.

BULL. 60:107-146.

ANDERSON, W. A. D.
1971. Degenerative changes and disturbances of metabolism. *In* W. A. D. Anderson (editor), Pathology, p. 68-95. The C. V. Mosby Co., St. Louis, 6th ed.

ARTHUR, D. K.
1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*. Fish. Bull., U.S. 74:517-530.
1977. Distribution, size, and abundance of microcopepods in the California Current system and their possible influence on survival of marine teleost larvae. Fish. Bull., U.S. 75: 601-611.

BALBONTIN, F., S. S. DE SILVA, AND K. S. EHRLICH.
1973. A comparative study of anatomical and chemical characteristics of reared and wild herring. Aquaculture 2:217-240.

BEERS, J. R., AND G. L. STEWART.
1967. Micro-zooplankton in the Euphotic zone at five locations across the California Current. J. Fish. Res. Board Can. 24: 2053-2068.
1970. Numerical abundance and estimated biomass of micro-zooplankton. *In* J. D. H. Strickland (editor), The ecology of the plankton off La Jolla, California, in the period April through September, 1967. Vol. 17 (Part VI), p. 67-87. Bull. Scripps Inst. Oceanogr.

BLAXTER, J. H. S.
1971. Feeding and condition of Clyde herring larvae. Rapp. P.-v. Réun. Cons. int. Explor. Mer 160:128-136.

BUCKLEY, L. J.
1980. Changes in the ribonucleic acid, deoxyribonucleic acid, and protein content during ontogenesis in winter flounder, *Pseudopleuronectes americanus*, and effect of starvation. Fish. Bull., U.S. 77:703-708.

CIECHOMSKI, J. D., DE, AND G. WEISS.
1974. Estudios sobre la Alimentacion de larvas de la merluza, *Merluccius merluccius* Hubbsi de la anchoita, *Engraulis anchoita*, en la mar. Physis. Secr. A Buenos Aires 33:199-208.

DEVONALD, K. F.
1983. Evaluation of the feeding success of first-feeding jack mackerel larvae off southern California, and some contributing factors. Ph.D. Thesis, Univ. California, Scripps Inst. Oceanogr., 227 p.

EHRLICH, K. F., J. H. S. BLAXTER, AND R. PEMBERTON.
1976. Morphological and histological changes during growth and starvation of herring and plaice larvae. Mar. Biol. (Berl.) 35:105-118.

ELLERTSEN, B., E. MOKSNESS, P. SOLENDAL, T. STRØMME, S. TILSETH, T. WESTGARD, AND V. ØIESTAD.
1981. Some biological aspects of cod larvae (*Gadus morhua* L.). ICES Symposium on Early Life History of Fish, Woods Hole, Mass., April 1979. Rapp. R.-v. Réun. Cons. int. Explor. Mer 178:317-319.

FARRIS, D. A.
1961. Abundance and distribution of eggs and larvae and survival of larvae of jack mackerel (*Trachurus symmetricus*). U.S. Fish Wildl. Serv., Fish. Bull. 61:247-279.

HAY, D. E.
1981. Effects of capture and fixation on gut contents and body size of Pacific herring larvae. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:395-400.

HEWITT, R., G. H. THEILACKER, AND N. C. H. LO.
In press. Causes of mortality in young jack mackerel. Mar. Ecol. Prog. Ser.

HJORT, J.
1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-v. Réun. Cons. Perm. int. Explor. Mer. 20:1-228.

HONJO, K., T. KITACHI, AND H. SUZUKI.
1959. On the food distribution and survival of post larval iwashi-1-Distribution of food organisms, the food of the anchovy and ecologically related species along the southwestern Pacific coast of Honshu, Sept.-Nov. 1958. Reports on the major coastal fish investigations, and the investigations for forecasting of oceanographic conditions and fisheries (preliminary report), February 1959. (Engl. Transl. by S. Hayaski.)

HUNTER, J. R.
1981. Feeding ecology and predation of marine fish larvae. *In* R. Lasker (editor), Marine fish larvae morphology, ecology and relation to fisheries, p. 33-77. Wash. Sea Grant Program, Univ. Wash. Press, Seattle.

HUNTER, J. R., AND C. SANCHEZ.
1976. Diel changes in swim bladder inflation of the larvae of the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 74:847-855.

HUNTER, J. R., J. H. TAYLOR, AND H. G. MOSER.
1979. Effects of ultraviolet irradiation on eggs and larvae of the northern anchovy, *Engraulis mordax*, and the Pacific mackerel, *Scomber japonicus*, during the embryonic stage. Photochem. Photobiol. 29:325-338.

IWAI, T.
1968. The comparative study of the digestive tract of teleost larvae—V. Fat. absorption in the gut epithelium of goldfish larvae. Bull. Jpn. Soc. Sci. Fish. 34:973-978.
1969. Fine structure of gut epithelial cells of larval and juvenile carp during absorption of fat and protein. Arch. Hist. Jpn. 30:183-199.

IWAI, T., AND M. TANAKA.
1968. The comparative study of the digestive tract of teleost larvae—III. Epithelial cells in the posterior gut of halfbeak larvae. Bull. Jpn. Soc. Sci. Fish. 34:44-48.

JONES, R., AND W. B. HALL.
1974. Some observations on the population dynamics of the larval stage in common gadoids. *In* J. H. S. Blaxter (editor), Early life history of fish, p. 87-102. Springer-Verlag. Berl.

LASKER, R.
1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453-462.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.
1970. Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345-353.

LO, N. C. H.
In press. Egg production of the central stock of northern anchovy, 1951-1982. Fish. Bull., U.S. 83.

LOVE, R. M.
1970. The chemical biology of fishes. Acad. Press (Lond.), p. 222-257.

MACCALL, A. D., AND G. D. STAUFFER.
1983. Biology and fishery potential of jack mackerel (*Trachurus symmetricus*). Calif. Coop. Oceanic Fish. Invest. Rep. 24:46-56.

MAY, R. C.
1974. Larval mortality in marine fishes and the critical period concept. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 3-19. Springer-Verlag, N.Y.

METHOT, R. D., JR.
1981. Growth rates and age distributions of larval and juvenile northern anchovy,, *Engraulis mordax*, with inferences on larval survival. Ph.D. Thesis, Univ. California, San Diego, 328 p.

METHOT, R. D., JR., AND D. KRAMER.
1979. Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. Fish. Bull., U.S. 77:413-423.

NAKAI, Z., M. KOSAKA, M. OGURA, G. HAYASHIDA, AND H. SHIMOZONO.
1969. Feeding habit, and depth of body and diameter of digestive tract of *Shirasu*, in relation with nutritious conditions. J. Coll. Mar. Sci. Technol., Tokai Univ. 3:23-34.

O'CONNELL, C. P.
1976. Histological criteria for diagnosing the starving condition in early post yolk sac larvae of the northern anchovy, *Engraulis mordax* Girard. J. Exp. Mar. Biol. Ecol. 25:285-312.
1980. Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods. Fish. Bull., U.S. 78:475-489.

RAJOS DE MENDIOLA, B. R.
1974. Food of the larval anchoveta, *Engraulis ringens* J. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 277-285. Springer-Verlag, N.Y.

SHELBOURNE, J. E.
1957. The feeding and condition of plaice larvae in good and bad plankton catches. J. Mar. Biol. Assoc. U.K. 36:539-552.

SMITH, P. E., AND S. L. RICHARDSON.
1977. Standard techniques for pelagic fish egg and larva surveys. F.A.O. Fish. Tech. Pap. 175, 100 p.

THEILACKER, G. H.
1978. Effect of starvation on the histological and morphological characteristics of jack mackerel, *Trachurus symmetricus*, larvae. Fish. Bull., U.S. 76:403-414.
1980a. Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. Fish. Bull., U.S. 78:685-692.
1980b. Rearing container size affects morphology and nutritional condition of larval jack mackerel, *Trachurus symmetricus*. Fish. Bull., U.S. 78:789-791.
1981. Effect of feeding history and egg size on the morphology of jack mackerel, *Trachurus symmetricus*, larvae. ICES Symposium on Early Life History of Fish, Woods Hole, Mass., April 1979. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:432-440.

THEILACKER, G. H., AND K. DORSEY.
1980. Larval fish diversity. *In* Workshop on the effects of environmental variation on the survival of larval pelagic fishes. Intergov. Oceanogr. Comm. Rep. 28:105-142. UNESCO, Paris.

UMEDA, S., AND A. OCHIAI.
1975. On the histological structure and function of digestive organs of the fed and starved larvae of the yellowtail, *Seriola quinqueradiata*. [In Jpn., Engl. summ.] Jpn. J. Ichthyol. 21:213-219.

WATANABE, Y.
1981. Ingestion of horseradish peroxidase by the intestinal cells in larvae or juveniles of some teleosts. Bull. Jpn. Soc. Sci. Fish. 47:1299-1307.

HYPOXIA IN LOUISIANA COASTAL WATERS DURING 1983: IMPLICATIONS FOR FISHERIES

MAURICE L. RENAUD[1]

ABSTRACT

Hypoxic bottom water (≤2.0 ppm dissolved oxygen) was present in shallow (9-15 m) waters south of central Louisiana in June and July 1983. It was patchy in distribution from south of Barataria Pass to south and west of Marsh Island. Data suggested that bottom water hypoxia did affect the abundance and distribution of shrimp and bottomfish. Offshore bottom water dissolved oxygen was significantly correlated with 1) combined catches of brown and white shrimp ($r = 0.56$, $P < 0.002$), 2) fish biomass ($r = 0.56$, $P < 0.001$), and 3) vertical density gradient ($r = -0.73$, $P < 0.001$). Several hypoxic stations were in regions designated as potentially hypoxic through a posteriori analysis of satellite data. *Micropogonius undulatus* was the dominant fish species nearshore and offshore. *Penaeus aztecus* and *P. setiferus* were sparsely distributed throughout the study area.

The presence of bottom water hypoxia (≤2.0 ppm dissolved oxygen) in the nearshore Gulf of Mexico is a common, recurring, and mostly seasonal (June-August) event. It is generally thought to be associated with temperature and salinity stratification initiated by freshwater runoff and with phytoplankton blooms during hot, calm weather (Fotheringham and Weissberg 1979; Bedinger et al. 1981; Comiskey and Farmer 1981; Turner and Allen 1982a, b; Boesch 1983; Leming and Stuntz 1984). Phytoplankton respiration and decomposition of sinking organic matter are major oxygen consuming processes. High oxygen demand of the organic load in freshwater runoff (Gallaway 1981) and lack of a direct oxygen replenishing mechanism (strong winds) in the presence of vertical stratification contribute to hypoxia formation (Harris et al. 1976; Ragan et al. 1978; Swanson and Sindermann 1979; Harper et al. 1981). Christmas (1973) and Boesch (1983) discussed possible nitrate pollution in rivers and coastal hypoxia. Boesch (1983) presented a brief history of hypoxia in the Gulf of Mexico and evaluated its causes and consequences. The extent to which any factor is involved with hypoxia formation is unknown.

Hypoxia in the Gulf of Mexico has been most noticeable in shallow (<20 m) Louisiana waters. It has been reported infrequently on the Texas shelf (Harper et al. 1981; Gallaway and Reitsema 1981). Low oxygen levels have also been measured east of the Mississippi River Delta inshore of barrier islands and in inland bays (May 1973; Christmas 1973) and offshore of Mobile Bay, AL (Turner and Allen 1982b). Abnormally high concentrations of moribund fish and crustaceans near the shoreline ("jubilees") in Alabama have also been linked to hypoxia (May 1973).

Considerable interest in hypoxia has been renewed by a less than average shrimp harvest in 1982 (Klima et al. 1983) and 1983[2]. In this paper I report the locations and extent of Louisiana coastal hypoxia in 1983 and discuss the interrelationships of fish and shrimp abundance and distribution with environmental parameters.

METHODS

Nearshore data were collected in a 7.3 m Aqua-Sport at a total of 56 stations from nine transects west of the Mississippi River Delta (long. 89°33′W to 90°14′W) from 1 to 16 June 1983 (Fig. 1). The transects, perpendicular to shore, ranged from 5 to 8 km in length and 1 to 16 m in depth. The six easternmost transects were sampled twice, with a sampling interval of 14 d. Shrimp and bottomfish were collected at 23 of 56 stations in 15-min tows with a 3.0 m box trawl. Towing speed was about 3 kn. Before each tow, water temperature, salinity, and dissolved oxygen concentration were recorded at 1 m depth intervals with a Hydrolab 8000. Hydrographic profiles were made at the remaining 33 stations.

An offshore study area extending from long.

[1]Southeast Fisheries Center Galveston Laboratory, National Marine Fisheries Service, NOAA, 4700 Avenue U, Galveston, TX 77550.

[2]1983 Gulf Coast Shrimp Data, NOAA, NMFS.

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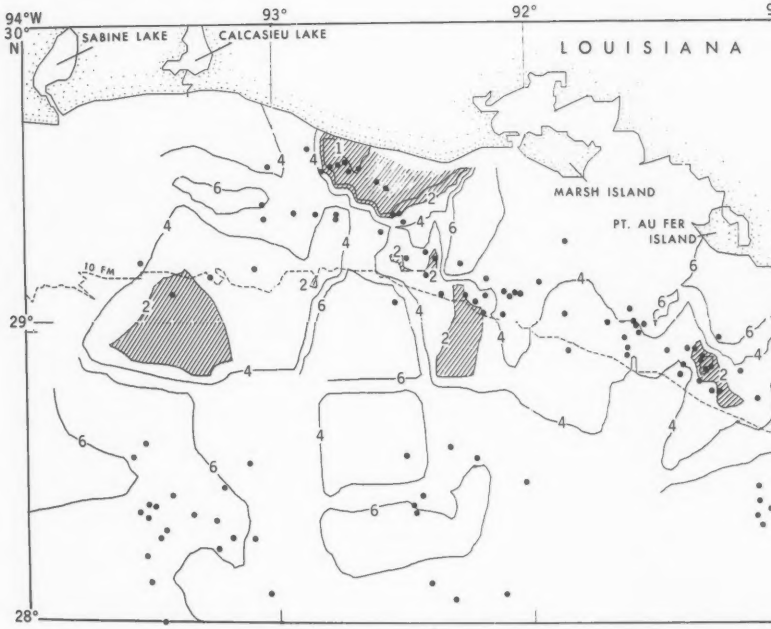

FIGURE 1.—Dissolved oxygen contours in Louisiana coastal waters, June-July 1983. Shaded portions repr

ns represent dissolved oxygen levels ≤2.0 ppm; solid circles are station locations.

90°47′W to 93°02′W was sampled with a 24.4 m steel-hull commercial shrimp trawler from 30 June to 6 July 1983 (Fig. 1). Depth varied from 4 to 20 m and distance from shore ranged from 8 to 54 km. Shrimp and bottomfish were collected at 34 of 65 stations in 20-min tows with a 12.2 m semiballoon trawl. The same trawl was used as a midwater shrimp sampler above previously identified hypoxic water. Surface and bottom measurements of water temperature, salinity, and dissolved oxygen concentration were recorded before each tow. Water samples were collected with a Kemmerer bottle. Salinities were measured with a refractometer. Temperature and dissolved oxygen concentration were measured with a YSI Model 51-B. Surface and bottom hydrographic data were collected at the remaining 31 stations. The Southeast Area Monitoring and Assessment Program (SEAMAP)[3] personnel collected similar data off Louisiana in June 1983. SEAMAP dissolved oxygen data were included in the contour analyses.

The Harvard SYMAP program (Dougenik and Sheehan 1975), a Northwest Alaska Fisheries Center Contour Subroutine, and the Galveston Laboratory Generalized Mapping system were utilized to produce a map of dissolved oxygen contours off Louisiana. Koi[4] presents an indepth explanation of these contour mapping programs. Vertical density gradient of the water column, shrimp catch, and fish catch were regressed with bottom water dissolved oxygen concentration. A "best fit" line through the data was determined using the least squares concept.

Surface water temperature (°C) and chlorophyll content (mg/m^3) were measured off Louisiana by the Coastal Zone Color Scanner (CZCS) aboard the Nimbus-7 satellite. Personnel from the Mississippi Laboratories of the Southeast Fisheries Center, working at the National Space Technology Laboratories, Mississippi, used CZCS and "ground truth" field data to predict potentially hypoxic areas in coastal Louisiana waters.

RESULTS AND DISCUSSION

Regions of hypoxic bottom water have been detected along portions of the Texas-Louisiana coastline every summer from 1972 to 1983 (Harris et al. 1976; Ragan et al. 1978; Bedinger et al. 1981; Harper et al. 1981; Reitsema et al. 1982; Boesch 1983). Hypoxia was noted from 16 June to 6 July 1983. It was patchy in distribution and found mainly in 9 to 15 m depths from south of Barataria Pass to south and west of Marsh Island (Fig. 1).

A total of 34 fish and 11 invertebrate species were collected offshore. The Atlantic croaker, *Micropogonius undulatus*, and the Atlantic threadfin, *Polydactylus octonemus*, were the dominant bottomfish at 58% and 30% of the stations, respectively; Atlantic bumper, *Chloroscombrus chrysurus*, was the common pelagic. Brown shrimp, *Penaeus aztecus*; white shrimp, *P. setiferus*; mantis shrimp, *Squilla empusa*; and broken-back shrimp, *Trachypenaeus* sp., were the most common invertebrates collected, but in small quantities. Total crustacean catch was always <5.0 kg/h.

Bottom water dissolved oxygen concentration was significantly correlated with 1) fish biomass (r = 0.56, $P < 0.001$) (Fig. 2) and the number of brown and white shrimp present (r = 0.56, $P < 0.002$) (Fig. 3). Shrimp and bottomfish were generally absent from hypoxic stations. Atlantic croaker were not at stations with hypoxic bottomwater, and shrimp catches never exceeded 2 kg/h in the areas. Sea catfish, *Arisus felis*; butterfish, *Peprilus paru*; and Atlantic bumper were common in trawls at hypoxic sites. These were also the most abundant fish in mid-

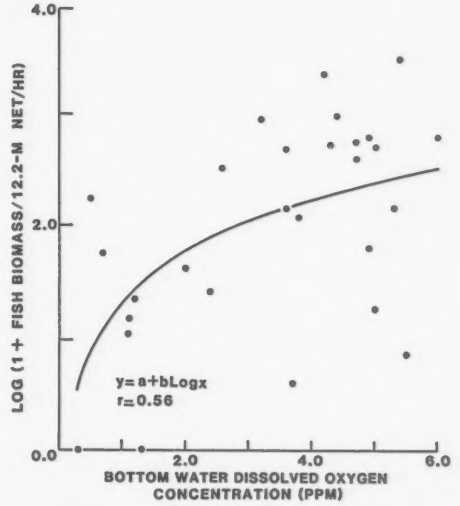

FIGURE 2.—Offshore fish biomass in relation to bottom water dissolved oxygen concentration.

[3]Southeast Area Monitoring and Assessment Program: a State-Federal cooperative research effort organized to assess the distribution and abundance of shrimp and bottomfish in the Gulf of Mexico.

[4]Koi, D. 1985. Generalized geographic mapping system. Unpubl. manuscr., 47 p. Southeast Fisheries Center Galveston Laboratory, National Marine Fisheries Service, NOAA, 4700 Avenue U, Galveston, TX 77550.

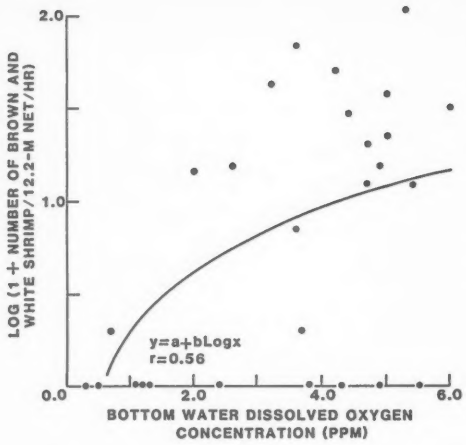

FIGURE 3.—Offshore shrimp abundance in relation to bottom water dissolved oxygen concentration.

water trawls above previously identified hypoxic areas. Therefore, it was concluded that they were captured from the upper water column as the trawl passed through it. Four brown shrimp, three lesser blue crabs, *Callinectes similus*, and one mantis shrimp were the only crustaceans captured in five midwater trawls. The relationship between shrimp and bottomfish abundance and distribution indicates that they do not pass through or over hypoxic water masses. Actual avoidance behavior in the field has not been documented.

Nearshore, a total of 20 fish and 5 invertebrate species were collected. Atlantic croaker was the dominant species. Brown shrimp were present in low numbers at most stations. White shrimp; blue crabs, *Callinectes sapidus*; lesser blue crabs; and sea bobs, *Xiphopenaeus* sp., were the only other crustaceans collected. A high variability in fish and shrimp abundance was probably due to the low fishing efficiency of the small net at the deeper nearshore stations. As a result, no significant correlation was present at nearshore stations between bottom water dissolved oxygen concentration and fish or shrimp abundance.

Vertical density stratification was present at both nearshore and offshore stations. Dissolved oxygen concentration and vertical density gradient were negatively correlated ($r = -0.73$, $P < 0.001$) (Fig. 4). This agrees with Leming and Stuntz (1984) who found a high correlation between bottom dissolved oxygen content and surface to bottom density gradients off Louisiana in 1982 ($r = -0.74$, $P < 0.001$). Offshore, the mean difference between surface and bottom dissolved oxygen was 6.4 ppm (standard error = 0.40) in hypoxic areas and 1.6 ppm (standard error = 0.08) in nonhypoxic areas. Temperature generally did not vary more than 2°C between the surface and bottom regardless of the area.

During the first week of July, 92% of the hypoxic stations were in areas predicted as potentially hypoxic through a posteriori analyses of remote sensing data. Hypoxic areas were characterized by surface water temperatures near 30°C, which agrees with Leming and Stuntz (1984). They discussed satellite data acquisition, its value in identifying and forecasting hypoxic regions in the Gulf of Mexico,

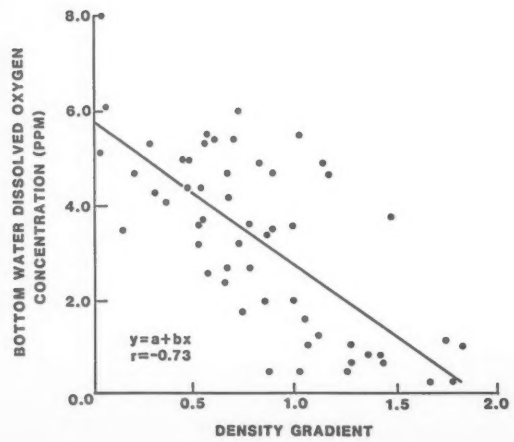

FIGURE 4.—Bottom water dissolved oxygen concentration in relation to vertical density gradient of the water column. Density gradient is expressed as (bottom sigma-t minus surface sigma-t)/depth.

and its implications regarding shrimp management.

The effect of hypoxia on shrimp is not completely understood. It is possible that an extensive area of hypoxic bottom water can act as a physical barrier to juvenile shrimp migration offshore and to postlarval migration into nursery grounds. Limited indirect evidence supports this hypothesis. Gazey et al. (1982) described a shrimp mark-release study in Louisiana. Extensive longshore and offshore movement occurred before the recapture of the shrimp during 1979, when hypoxia was not reported off Louisiana (Fig. 5). In 1978, when hypoxia was widespread along the Louisiana coastline (Fig. 6), shrimp did not move comparable distances. It was possible that hypoxia reduced shrimp movement into offshore waters.

The most extensive occurrence of hypoxic bottom water recorded in Louisiana coastal waters occurred from May 1973 to May 1974 (Flowers et al. 1975; Ragan et al. 1978). It was widespread between Barataria and Timbalier Passes and extended up to 30 km offshore in some regions. Ragan et al. (1978) reported several areas to be anoxic. The duration and severity of this hypoxic condition may have had an impact on the offshore brown shrimp fishery in 1973.

Total brown shrimp catch and CPUE (catch per unit effort) in 1973 were significantly lower (paired t-test, $P < 0.05$) than in 1972 (fn. 2). Catch declined 36% (2.8 million kg) and the mean CPUE was reduced by 120 kg/vessel per d. Movement of juvenile brown shrimp to the offshore fishery occurs from May to August (Cook and Lindner 1970). Monthly catch and CPUE of brown shrimp from January through April 1973 did not differ from the same time period in 1972; however, catch and CPUE from May through December were significantly lower (paired t-test, $P < 0.01$) in 1973. Postlarval recruitment of brown shrimp occurs from January to May (Baxter and Renfro 1966). An interaction between hypoxia and postlarval recruitment in 1974 might have been responsible for the continued poor harvest of brown shrimp that year. Catch and CPUE were still significantly lower than in 1972 (paired t-test, $P < 0.05$). It was not until 1976 that brown shrimp catch surpassed the 1972 levels (Table 1). A decline in total shrimp catch of Louisiana in 1982 may have been related to a large region of hypoxic bottom water reported by Stuntz et al. (1982).

Although hypoxia has not been directly linked to declines in annual catch, its presence during critical

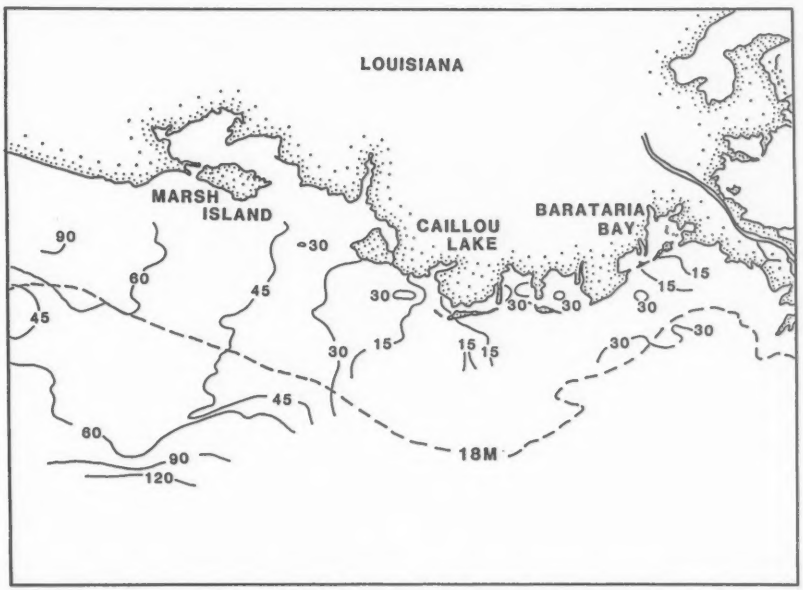

FIGURE 5.—Movement of tagged juvenile brown shrimp from Caillou Lake and Barataria Bay expressed as days at large before recapture (from Gazey et al. 1982). Shrimp were released in July 1979. Hypoxia was not documented off this coastal area in 1979.

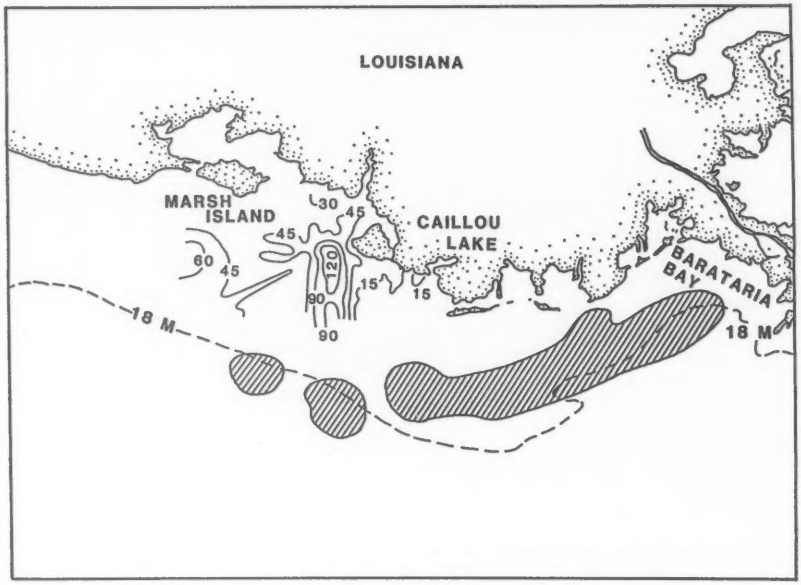

FIGURE 6.—Movement of tagged juvenile brown shrimp from Caillou Lake, expressed as days at large before recapture (from Gazey et al. 1982). Shrimp were released in June 1978. Regions of hypoxic bottom water, noted from June to August, are overlaid onto this map (Fotheringham and Weissberg 1979; Bedinger et al. 1981; Comiskey and Farmer 1981).

TABLE 1.—Louisiana brown shrimp catch data.

		1972	1973	1974	1975	1976	5-yr average
Catch per unit effort (kg/vessel per d)	Jan.-Apr.	190	216	180	196	208	198
	May-Aug.	383	225	249	296	348	300
	Sept.-Dec.	376	233	328	346	268	310
	Annual average	344	[1]223	[1]256	288	302	284
Catch (millions of kg)	Jan.-Apr.	0.831	1.478	0.633	0.645	1.020	0.921
	May-Aug.	4.529	2.630	2.702	2.112	5.966	3.588
	Sept.-Dec.	2.293	0.822	1.578	1.414	2.601	1.742
	Total	7.653	[1]4.930	[1]4.913	4.171	9.587	6.251
Effort (24-h days fished)	Jan.-Apr.	4,379	6,870	3,509	3,288	4,903	4,590
	May-Aug.	11,828	11,722	10,852	7,128	17,127	11,731
	Sept.-Dec.	6,361	3,528	4,805	4,083	9,715	5,698
	Total	22,568	22,120	19.166	14,499	31,745	22,020

[1]CPUE and catch data in 1973 and 1974 were significantly lower than that in 1972 (paired *t*-test, $P < 0.05$).

portions of the shrimp life cycle implicate it as a probable source of variation in annual shrimp yield. Support for this viewpoint has been documented in laboratory experiments which indicate that brown and white shrimp detect and avoid water with low oxygen levels.[5] Brown shrimp were the least tolerant of the two species. They avoided dissolved oxygen concentrations up to and including 2.0 ppm. White shrimp did not avoid oxygen levels higher than 1.5 ppm. Variable behavior was exhibited by both species at higher treatment levels. Total time (TT) spent in water with 1.5 ppm did not differ between species,

[5]Renaud, M. 1985. Detection and avoidance of oxygen depleted water by *Penaeus setiferus* and *Penaeus aztecus*. Unpubl. manuscr., 16 p. Southeast Fisheries Center Galveston Laboratory, National Marine Fisheries Service, NOAA, 4700 Avenue U, Galveston, TX 77550.

nor did their response time (RT), i.e., time taken to retreat into normal seawater. However, these measurements were significantly (t-test, $P < 0.001$) shorter for brown shrimp (TT = 6.2, RT = 3.8 min) versus white shrimp (TT = 20.0, RT = 6.2 min) when tested at 2.0 ppm. Behavioral responses of brown and white shrimp exposed to hypoxic water included 1) an initial increase in activity, 2) walking or swimming retreat, and 3) rapid eye movements. White shrimp also exhibited notable abdominal flexing, periods of exhaustion, and sometimes death. These three latter behaviors were not observed with brown shrimp. Dissolved oxygen levels tested are common along Louisiana's Gulf Coast during the summer and early fall. Therefore it is not unreasonable to assume that similar behavioral responses occur in nature.

Hypoxia in the New York Bight (Swanson and Sindermann 1979) had a severe impact on the commercial fisheries of sedentary species. Surf clam, *Spisula solidissima*; ocean quahog, *Arctica islandica*; and scallop, *Placopectin magellanicus*, abundance was reduced by 92%, 25%, and 12%, respectively, in the affected area. The response of recreational fish species, summer flounder, *Paralichthys dentatus*, and bluefish, *Pomatomus saltatrix*, to low oxygen levels was noted by changes in their distribution patterns during the hypoxic event. Temperature stratification, phytoplankton blooms, spoil deposition, and sewage treatment outflow were alleged major contributors to hypoxia formation in the New York Bight. It was concluded, however, that abnormal climatological and hydrological phenomena were responsible for this hypoxic event. Swanson and Sindermann (1979) stated that effective regulation of waste disposal into riverine and oceanic environments may control or restrict bottom water hypoxia formation.

Future research on the phenomenon of hypoxia should be centered on its predictability; remote sensing has potential in this area. Timely information dissemination on the extent and location of hypoxic areas would help fishermen to avoid areas where low catches might be anticipated or to harvest a crop before it dies or migrates.

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LITERATURE CITED

BAXTER, K. N., AND W. C. RENFRO.
1966. Seasonal occurrence and size distribution of postlarval brown and white shrimp near Galveston, Texas, with notes on species identification. U.S. Fish Wildl. Serv., Fish. Bull. 66:149-158.

BEDINGER, C. A., R. E. CHILDERS, J. W. COOPER, K. T. KIMBALL, AND A. KWOK.
1981. Pollution fate and effect studies. *In* C. A. Bedinger (editor), Ecological investigations of petroleum production platforms in the central Gulf of Mexico, Vol. 1, Part 1, 53 p. Report to the Bureau of Land Management, New Orleans, LA, Contract No. AS551-CT8-17.

BOESCH, D. F.
1983. Implications of oxygen depletion on the continental shelf of the northern Gulf of Mexico. Coastal Ocean Pollut. Assess. News 2:25-28.

CHRISTMAS, J. Y. (editor).
1973. Cooperative Gulf of Mexico estuarine inventory and study, Mississippi: Phase I, area description, Phase II, hydrology, Phase II, sedimentology, Phase IV, biology. Gulf Coast Research Laboratory, Ocean Springs, MS, 434 p.

COMISKEY, C. E., AND T. A. FARMER (editors).
1981. Characterization of base-line oceanography for the Texoma region brine disposal sites. Vol. I. Final Report to U.S. Department of Energy, Strategic Petroleum Reserve Office, Wash., D.C., Contract No. DEAC01-774508788, 130 p.

COOK, H. L., AND M. J. LINDNER.
1970. Synopsis of biological data on the brown shrimp *Penaeus aztecus aztecus* Ives, 1891. *In* M. N. Mistakidis (editor), Proceedings of the World Scientific Conference on the Biology and Culture of Shrimps and Prawns, p. 1471-1497. FAO Fish. Rep. 57(4).

DOUGENIK, J. A., AND D. E. SHEEHAN.
1975. SYMAP User's Manual. Camera Stat of Bedford, Cambridge, MA, 187 p.

FLOWERS, C. W., W. T. MILLER, AND J. D. GANN.
1975. Water chemistry. *In* J. G. Gosselink, R. H. Miller, M. Hood, and L. M. Bahr (editors), Environmental assessment of a Louisiana offshore port and appertinent pipeline and storage facility. Vol. II, App. V, Sect. 1, 86 p. Final Report to Louisiana Offshore Oil Port, New Orleans, LA.

FOTHERINGHAM, N., AND G. H. WEISSBERG.
1979. Some causes, consequences and potential environmental impacts of oxygen depletion in the northern Gulf of Mexico. Proc. 11th Annu. Offshore Tech. Conf., April 30-May 3, 1979, 3611:2205-2208.

GALLAWAY, B. J.
1981. An ecosystem analysis of oil and gas development on the Texas-Louisiana continental shelf. U.S. Fish Wildl. Serv., Off. Biol. Serv., Wash., D.C., FWS/OBS-81-27, 88 p.

GALLAWAY, B. J., AND L. A. REITSEMA.
1981. Shrimp spawning site survey. *In* W. B. Jackson and E. P. Wilkens (editors), Shrimp and redfish studies; Bryan Mound brine disposal site off Freeport, Texas 1979-1981.

NOAA Tech. Memo. NMFS-SEFC-67, Vol. IV, 84 p. Available from National Technical Information Service, Springfield, VA 22151.

GAZEY, W. J., B. J. GALLAWAY, R. C. FECHHELM, L. R. MARTIN, AND L. A. REITSEMA.
1982. Shrimp mark release and port interview sampling survey of shrimp catch and effort with recovery of captured tagged shrimp. *In* W. B. Jackson (editor), Shrimp population studies: West Hackberry and Big Hill brine disposal sites off southwest Louisiana and upper Texas coasts, 1980-1982, Vol. II, 306 p. NOAA/NMFS Final Report to Department of Energy.

HARPER, D. E., L. D. MCKINNEY, R. R. SALZER, AND R. J. CASE.
1981. The occurrence of hypoxic bottom water off the upper Texas coast and its effects on the benthic biota. Contrib. Mar. Sci. 24:53-79.

HARRIS, A. H., J. G. RAGAN, AND R. H. KILGEN.
1976. Oxygen depletion on coastal waters. La. State Univ. Sea Grant Summ. Rep., Proj. No. R/BOD-1, 161 p.

KLIMA, E. F., K. N. BAXTER, F. J. PATELLA, AND G. A. MATTHEWS.
1983. Review of 1982 Texas closure for the shrimp fishery off Texas and Louisiana. NOAA Tech. Memo. NMFS-SEFC-108, 22 p. Available from National Technical Information Service, Springfield, VA 22151.

LEMING, T. D., AND W. E. STUNTZ.
1984. Zones of coastal hypoxia revealed by satellite scanning have implications for strategic fishing. Nature (Lond.) 310: 136-138.

MAY, E. B.
1973. Extensive oxygen depletion in Mobile Bay, Alabama. Limnol. Oceanogr. 18:353-366.

RAGAN, J. G., A. H. HARRIS, AND J. H. GREEN.
1978. Temperature, salinity and oxygen measurements of surface and bottom waters on the continental shelf off Louisiana during portions of 1975 and 1976. Nicholls State Univ., Prof. Pap. Ser. (Biol.) 3:1-29.

REITSEMA, L. A., B. J. GALLAWAY, AND G. S. LEWBEL.
1982. Shrimp spawning site survey. *In* W. B. Jackson (editor), Shrimp population studies: West Hackberry and Big Hill brine disposal sites off southwest Louisiana and upper Texas coasts, 1980-1982, Vol. IV, 88 p. NOAA/NMFS Final Report to Department of Energy.

STUNTZ, W. E., N. SANDERS, T. D. LEMING, K. N. BAXTER, AND R. M. BARAZOTTO.
1982. Area of hypoxic bottom water found in northern Gulf of Mexico. Coastal Ocean. Climatol. News 4:37-38.

SWANSON, R. L., AND C. J. SINDERMANN (editors).
1979. Oxygen depletion and associated benthic mortalities in New York Bight, 1976. NOAA Prof. Pap. No. 11, 345 p. Rockville, MD.

TURNER, R. E., AND R. L. ALLEN.
1982a. Bottom water oxygen concentration in the Mississippi River Delta Bight. Contrib. Mar. Sci. 25:161-172.
1982b. Plankton respiration rates in the bottom waters of the Mississippi River Delta Bight. Contrib. Mar. Sci. 25:173-179.

INCIDENTAL MORTALITY OF DOLPHINS IN THE EASTERN TROPICAL PACIFIC, 1959-72

N. C. H. Lo[1] AND T. D. Smith[2]

ABSTRACT

The estimates of the number of dolphins killed annually from the beginning of the U.S. tuna purse seine fishery in the eastern tropical Pacific are used by the National Marine Fisheries Service in developing management advice for the U.S. purse seine fleet. We estimated the annual number of dolphins killed incidentally in the tuna purse seine fishery for 1959-72. Kill data were available for only a few years prior to 1970. Because no obvious trend was shown with the existing data, kill rates were averaged over those years and stratified by various categories: large and small vessels, sets with large catch of tuna and small catch of tuna, sets which used backdown (a dolphin-releasing procedure), and sets which did not use backdown. These kill rates, combined with estimated number of sets, produced the estimated annual kills. Because data were available only for some of the years, they had to be pooled to obtain annual estimates. As a result, the annual estimates were highly correlated. Because the total as well as the annual estimates are of interest, it is necessary to compute the variance-covariance of the estimated annual kills. The annual kill from 1959 to 1972 varied from 55,000 in 1959 to 534,000 in 1961. There were three distinct maxima of 534,000, 460,000, and 467,000, corresponding to peaks in number of sets made on dolphins in 1961, 1965, and 1970. The total kill from 1959 to 1972 was estimated to be about 4.8 million, with a coefficient of variation of 17%.

The eastern tropical Pacific tuna purse seine fleet began to develop rapidly in the late 1950's and has grown to over 100 U.S.-registered vessels and a substantial number of non-U.S.-registered vessels in recent years. This fleet fishes primarily for yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Katsuwonus pelamis*. Majority of the yellowfin tuna are taken while the tunas are schooling with dolphins primarily of the species *Stenella attenuata* and *S. longirostris*. Birds and dolphins are frequently used as cues in finding the tuna. During the capture of the tuna, some of the dolphins are killed or drowned by becoming tangled in the net webbing (Perrin 1969). The number of dolphins killed has been estimated to have been greater than one-half million in some of the years in the 1960's (Smith 1983). Currently, fewer animals are killed each year due to improvements in the fishing gear and in procedures to release dolphins.

Estimates of the total number of dolphins killed each year in this fishery are used as a basis for management advice by the National Marine Fisheries Service (NMFS). In this paper we describe in detail the method used in Smith (1983), including estimation of the variances and covariances of the annual kill estimates so that the variance of the total kill for the period can be estimated. Additionally, we reexamine the data used in previous estimates (Perrin 1970; Perrin and Zweifel 1971[3]; Perrin et al. 1982; Smith 1983; Smith and Lo 1983), and we present revised estimates of the total numbers of dolphins killed.

MATERIALS AND METHODS

The model used to estimate the total annual incidental kill of dolphins (T_t) in the eastern tropical Pacific tuna purse seine fishery is

$$\hat{T}_t = \hat{R}_t \hat{X}_t \qquad (1)$$

where t denotes the year (1959 to 1972), R denotes the number of dolphins killed per set, and X denotes the number of sets made involving dolphins. The rate of kill (R) varies between larger and smaller vessels, and in dolphin sets where fewer and greater amounts of yellowfin tuna are caught (Lo et al. 1982). In addition, the rate of dolphin kills is generally less if

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.
[2]Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[3]Perrin, W. F., and J. R. Zweifel. 1971. Porpoise mortality in the eastern tropical tuna fishery in 1971. Unpubl. manuscr., 22 p. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

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backdown, a dolphin-release procedure, is used (Green et al. 1971; Barham et al. 1977; Smith and Lo 1983). To account for these factors affecting rates of dolphin kill, Equation (1) can be reexpressed with the rates and numbers of sets stratified by vessel tuna carrying capacity, catch of fish, and use of backdown procedure:

$$\hat{T}_t = \sum_{i=1}^{2} \sum_{j=1}^{2} \sum_{k=1}^{2} \hat{R}_{tijk} \hat{X}_{tijk} \qquad (2)$$

where t = year
i = 1 for vessel capacity >600 tons; 2 for vessel capacity ⩽600 tons
j = 1 for yellowfin tuna catch ⩾¼ ton; 2 for yellowfin tuna catch <¼ ton
k = 1 backdown is used; 2 backdown is not used.

Data on the number of dolphins killed during fishing trips in the period from 1964 to 1968 are given in Smith and Lo (1983). Similar but more extensive data (e.g., backdown information) are available in NMFS records for 1971 and 1972. Estimates on the number of sets involving dolphins from 1959 to 1972 are given by Punsley (1983). These data sources have certain limitations which do not allow for the use of the complete stratification scheme in Equation (2). Assumptions are made based on sample sizes and on apparent lack of changes in rates over time to accommodate these limitations.

The mean numbers of dolphins killed (kill-per-set) are shown in Table 1 for each year in which data are available, stratified by vessel size and by catch of fish (successful, ⩾¼ ton of yellowfin tuna; unsuccessful, <¼ ton of yellowfin tuna). The definition of successful set follows that of Perrin and Zweifel (fn. 3). The vessel class stratification was based on the vessel's fish carrying capacity. The 1964-74 kill data indicate that kill-per-set was different for vessels with ⩽600 tons carrying capacity and vessels with >600 tons for unsuccessful sets. For successful sets the optimal vessel class stratification was not clear; either 400, 600, or 800 tons can be used as division points for stratification. For consistency, we adopted the same stratification used for unsuccessful sets. (The results were similar with alternative stratification schemes.) Other factors such as the age of the vessel and the experience of the captain could affect kill rates but were not considered in the stratification because these factors could not be isolated for analysis.

The mean number of dolphins killed varied markedly over the years but without any obvious trends (Table 1). A two-way analysis of variance with the data pooled over years showed statistically significant differences in kill rates in sets made by small and large vessels ($P < 0.01$) and in successful and unsuccessful sets ($P < 0.01$). Thus Equation (2) was simplified by eliminating the time stratification for kill rates, whereas the vessel size and catch strata were retained.

Few observations are available for sets where backdown was not used. In successful sets, backdown was used more than 90% of the time; thus, we have observations on kill rates in only 20 sets where backdown was not used. Thirteen of these sets were made by large vessels and seven by small vessels, and the mean kill rates within vessel size class are highly variable and not significantly different. The overall ratio of the kill rates, pooled over vessel size, when backdown was not used and when it was used is significantly greater than unity, and the annual

TABLE 1.—Average numbers of dolphins killed (*M*) in purse seine sets in the eastern tropical Pacific by year, for small and large vessels making successful (>¼ ton tuna) and unsuccessful (⩽¼ ton tuna) net sets. Standard deviation (SD), number of sets (*N*), and number of trips are given.

Vessels and year	Successful sets				Unsuccessful sets				Data source
	M	SD	*N*	No. of trips	*M*	SD	*N*	No. of trips	
Small vessels (⩽600 tons carrying capacity)									
1964	60	47	20	1	60	—	1	1	Smith and Lo (1983)[1]
1965	26	28	35	1	3	8	11	1	Smith and Lo (1983)
1968	130	114	13	1	4	4	2	1	Smith and Lo (1983)
1971	117	180	19	3	13	10	3	2	Unpubl. NMFS
1972	57	110	103	6	4	10	16	5	Unpubl. NMFS
Total	62	108	190	12	6	13	33	10	
Large vessels (>600 tons carrying capacity)									
1971	41	56	16	2	—	—	—	0	Unpubl. NMFS
1972	37	123	117	6	0.4	1.4	12	5	Unpubl. NMFS
Total	37	119	133	8	0.4	1.4	12	5	

[1]From table 5 of Smith and Lo (1983), omitting incomplete data collected in 1966.

ratios vary without a consistent trend over time (Table 2).

In unsuccessful sets the use of the backdown procedure was more variable because the conditions of the set are more diverse. For example, only a few or no dolphins may be captured, and the net may not be retrieved in the usual manner. Because of this diversity and because so few observations are available, we consider one kill rate for all unsuccessful sets.

Reexpressing Equation (2) to account for a constant ratio of kill rates for successful sets when backdown was used and when it was not used, and for no difference in kill rates for unsuccessful sets, yields

$$\hat{T}_t = \sum_{i=1}^{2}\sum_{j=1}^{2}\sum_{k=1}^{2} \hat{R}_{\bullet ijk}\hat{X}_{tijk}$$

$$= \sum_{i=1}^{2} \{\hat{R}_{\bullet i11}(\hat{X}_{ti11} + C\hat{X}_{ti12}) + \hat{R}_{\bullet i2\bullet}\hat{X}_{ti2\bullet}\} \quad (3)$$

where $C = R_{\bullet\bullet 12}/R_{\bullet\bullet 11}$ and the subscript $\bullet$ is used when that stratifying variable is not considered. For example, $R_{\bullet ijk}$ is the kill-per-set not stratified by year t, and $X_{ti2\bullet}$ is the total number of sets not stratified by use of backdown.

Estimates of the total number of sets involving dolphins from 1959 to 1972, with approximate variances, are given by Punsly (1983). He also gives partial estimates of the numbers of successful and unsuccessful sets, but does not provide estimates of the numbers of sets by vessel size. Punsly's data did not indicate the use of the backdown procedure.

The coefficients of variation (CV) of Punsly's estimates are ≤1% in all years except 1959 and 1960, when it was 8%. The percentage of unidentified sets in 1959-61 was higher than subsequent years because set type was not recorded systematically (Hammond[4]). We assume these estimates are in fact constants, because in most years, and in the absence of additional information in 1959-61, the CVs are small compared with the CVs of the kill rates (0.13-1.0, Table 1).

By applying the proportions of successful and unsuccessful dolphin sets from Punsly's partial estimates to his totals, we obtained numbers of successful and unsuccessful dolphin sets. We further prorate these estimated numbers of successful and unsuccessful sets to large and small vessels by multiplying by the estimates of proportions from NMFS (Anonymous 1976[5]) of sets made by vessels of each size class (Table 3). The slight differences between the totals for each year given by Punsly are due to rounding.

The number of sets during which backdown was used can be estimated from the estimated total number of sets involving dolphins (Table 3) and the observed proportion of successful sets in which backdown was used (Table 2). The observed proportions increase from 0.79 in 1964-65 to almost unity (0.96) by 1972. The backdown procedure was reportedly

[4]P. S. Hammond, Sea Mammal Research Unit, British Antarctic Survey, Cambridge, England, pers. commun. 1983.

[5]Anonymous. 1976. Report of the workshop on stock assessment of porpoises involved in the eastern Pacific yellowfin tuna fishery (La Jolla, July 27-31, 1976). Southwest Fish. Cent., Admin. Rep. LJ-76-29, 54 p. + app.

TABLE 2.—Mean number of dolphins killed ($\hat{R}$) during purse seine sets in the eastern tropical Pacific Ocean when the backdown dolphin-release procedure was and was not used. Also given are the ratio of numbers killed with and without backdown ($\hat{C}$), the proportion of successful sets where backdown was used ($\hat{P}$), the number of sets (N), number of trips, and standard error in parentheses.

	Backdown used							
	Yes			No				
Year	$\hat{R}_{t\bullet 11}$	N	No. of trips	$\hat{R}_{t\bullet 12}$	N	No. of trips	$\hat{C}$	$\hat{P}$
1964[1]	44	16	1	128	4	1	3.0	0.79
1965[1]	48	6	1	24	2	1	0.50	
1966[1,2]	—	17	1	—	2	1	—	0.89
1968[1]	142	11	1	92	1	1	0.65	
1971[3]	81	30	5	111	4	3	1.40	
1972[3]	41	193	12	169	9	6	4.10	0.96
Total	50	256	21	131	20	12	2.62	0.93
							[4](0.80)	

[1]From Smith and Lo (1983).
[2]Kill rates for 1966 omitted because incomplete data were collected.
[3]NMFS records.
[4]$SE(\hat{C}) = \hat{C}\,[CV^2(\hat{R}_{\bullet\bullet 12}) + CV^2(\hat{R}_{\bullet\bullet 11}) - 2\,\mathrm{cor}(\hat{R}_{\bullet\bullet 12}, \hat{R}_{\bullet\bullet 11})]^{1/2}$; where $\hat{C} = \hat{R}_{\bullet\bullet 12}/\hat{R}_{\bullet\bullet 11}$.

TABLE 3.—Numbers of purse seine sets involving dolphins in the eastern Pacific Ocean, from 1959 to 1972, for small (≤600 tons) and large (>600 tons) vessels, and for successful (>¼ tons tuna) and unsuccessful (≤¼ tons) sets, modified from Punsly (1983).

	Successful sets		Unsuccessful sets	
Year	small ($X_{t21\bullet}$)	large ($X_{t11\bullet}$)	small ($X_{t22\bullet}$)	large ($X_{t12\bullet}$)
1959	326	0	265	0
1960	3,170	0	2,303	0
1961	3,888	32	3,928	0
1962	1,773	5	1,942	19
1963	2,291	10	2,092	23
1964	4,444	45	3,089	64
1965	5,346	27	2,418	29
1966	4,948	44	1,835	25
1967	3,363	2	841	3
1968	2,956	175	982	41
1969	5,365	1,401	1,402	192
1970	4,936	2,313	957	412
1971	1,871	2,602	652	409
1972	2,704	4,982	855	846

developed on one vessel in 1959-60 (Barham et al. 1977) and used by at least three vessels in 1961 (Anonymous 1962). If 79% of the sets in 1964-65 were made using this procedure, as suggested by the very limited available data, a rather rapid increase in usage must have occurred in 1962 and 1963. This is possible because, if properly used, the procedure reduces the amount of handling time of dead dolphins, thus speeding up the fishing operation. As an approximation, we assume that usage increased from 0 to 0.79 linearly from 1959 to 1964-65, and was 0.89 for 1966-71 and 0.96 for 1972.

Denoting the interpolated and extrapolated estimates of the proportion of successful sets using the backdown dolphin release procedure by P_t gives

$$\hat{X}_{ti11} = \hat{P}_t \hat{X}_{ti1\bullet}$$

$$\hat{X}_{ti12} = (1 - \hat{P}_t)\, \hat{X}_{ti1\bullet}.$$

Substituting these relationships into Equation (3), with the assumption that the estimated numbers of sets given by Punsley (1983) are constants, the following equations result when the terms are rearranged:

$$\hat{T}_t = \sum_i \{\hat{R}_{\bullet i11}[X_{ti1\bullet}\hat{P}_t + C(1 - \hat{P}_t)X_{ti1\bullet}] + R_{\bullet i2\bullet}X_{ti2\bullet}\}$$

$$= \sum_i \{\hat{R}_{\bullet i11}X_{ti1\bullet}[\hat{P}_t + C(1 - \hat{P}_t)] + \hat{R}_{\bullet i2\bullet}\, X_{ti2\bullet}\}. \quad (4)$$

The time series of estimated annual kill ($\hat{T}_t$) from 1959 to 1972 was obtained by pooling the available data over years and strata, resulting in estimates that are not statistically independent. Thus in order to estimate the variance of the total kill of dolphins for the period in addition to the variances it is necessary to determine the covariances among the annual estimates.

We denote the estimates of the total kill of dolphins ($\hat{T}_t$) for each year from 1959 to 1972 by the vector $\hat{T}$, and denote the estimates of the variances of the elements of $\hat{T}$ by the symmetric matrix $\Sigma_{\hat{T}}$. The estimate of the kill in each year (Equation (4)) can be expressed in matrix form as the product of a vector of the numbers of sets in each of the four combinations of the vessel size and fishing success classifications (X_t), and a vector of the four corresponding kill rates (Q_t). Each element of $\hat{T}$ then can be expressed as a matrix product

$$\hat{T}_t = X'_t\, \hat{Q}_t \quad (5)$$

where $X'_t = (X_{t11\bullet}, X_{t21\bullet}, X_{t12\bullet}, X_{t22\bullet})$

$$\hat{Q}_t = \begin{bmatrix} \hat{Q}_{t1} \\ \hat{Q}_{t2} \\ \hat{Q}_{t3} \\ \hat{Q}_{t4} \end{bmatrix} = \begin{bmatrix} \hat{R}_{\bullet 111}[\hat{P}_t(1 - \hat{C}) + \hat{C}] \\ \hat{R}_{\bullet 211}[\hat{P}_t(1 - \hat{C}) + \hat{C}] \\ \hat{R}_{\bullet 12\bullet} \\ \hat{R}_{\bullet 22\bullet} \end{bmatrix} = \begin{bmatrix} \hat{R}_{\bullet 111} f_t \\ \hat{R}_{\bullet 211} f_t \\ \hat{R}_{\bullet 12\bullet} \\ \hat{R}_{\bullet 22\bullet} \end{bmatrix} \text{ and } f_t = \hat{P}_t(1 - \hat{C}) + \hat{C}.$$

Then the variance-covariance matrix of $\hat{T}$ is

$$\Sigma_{\hat{T}} = \begin{bmatrix} V(\hat{T}_{59}) & & & \\ \mathrm{Cov}(\hat{T}_{59}, \hat{T}_{60}) & V(\hat{T}_{60}) & & \\ \vdots & \vdots & & \\ \mathrm{Cov}(\hat{T}_{59}, \hat{T}_{72}) & \mathrm{Cov}(\hat{T}_{60}, \hat{T}_{72}) & \cdots & V(\hat{T}_{72}) \end{bmatrix}$$

$$= \begin{bmatrix} V(X'_{59}\, Q_{59}) & & & \\ \mathrm{Cov}(X'_{59}\, Q_{59}, X'_{60}\, Q_{60}) & V(X'_{60}\, Q_{60}) & & \\ \vdots & \vdots & & \\ \mathrm{Cov}(X'_{59}\, Q_{59}, X'_{72}\, Q_{72}) & \mathrm{Cov}(X'_{60}\, Q_{60}, X'_{72}\, Q_{72}) & \cdots & V(X'_{72}\, Q_{72}) \end{bmatrix}$$

with $V(\hat{T}_t) = X'_t \Sigma_{\hat{Q}_t} X_t$
as the diagonal elements of $\Sigma_{\hat{T}}$ (6)

where $\Sigma_{\hat{Q}_t} = \begin{bmatrix} V(\hat{R}_{\bullet 111} f_t) & \mathrm{Cov}(\hat{R}_{\bullet 111} f_t, \hat{R}_{\bullet 211} f_t) & 0 & 0 \\ & V(\hat{R}_{\bullet 211} f_t) & 0 & 0 \\ & & V(\hat{R}_{\bullet 21\bullet}) & 0 \\ & & & V(\hat{R}_{\bullet 22\bullet}) \end{bmatrix}$. (7)

The diagonal elements of $\Sigma_{\hat{T}}$ can be computed by noting that $\hat{R}_{\bullet i2\bullet}$ is uncorrelated with $\hat{R}_{\bullet i11}$, $\hat{P}_t$, or $\hat{C}$, and the covariance of $\hat{P}_t$ and $\hat{C}$ is zero because one C value is used for all years in 1959-72 and $\hat{P}_t$ can be different between years.

The off-diagonal elements of $\Sigma_{\hat{T}}$ are

$$\mathrm{Cov}(\hat{T}_u, \hat{T}_m) = \mathrm{Cov}(X'_u \hat{Q}_u, X'_m \hat{Q}_m) \quad (8)$$

$$= \sum_{i=1}^{4} \sum_{j=1}^{4} X_{ui}\, \mathrm{Cov}(\hat{Q}_{ui}, \hat{Q}_{mj})\, X_{mj}.$$

Expressions for each of the terms in $\Sigma_{\hat{T}}$ are given in the Appendix.

RESULTS AND DISCUSSION

The estimates of the total number of dolphins killed incidentally in the tuna purse seine fishery from 1959 to 1972 (Table 4, from Equation (4)) vary from a low of 55,000 in 1959 to a high of 534,000 in 1961. Three distinct maxima of 534,000, 460,000, and 467,000 are apparent (Fig. 1), corresponding to peaks in numbers of sets made on dolphins in 1961, 1965, and 1970 (Table 3). A total of about 4.8 million dolphins is estimated to have been killed in the whole period (Table 4).

The CVs of the annual estimates decline rapidly

TABLE 4.—Estimated number of dolphins killed by year (Equation (4)), with standard errors (SE) and coefficient of variations (CV).

Year	Number killed	SE	CV
1959	55,000	18	0.32
1960	478,000	146	0.31
1961	534,000	149	0.28
1962	216,000	54	0.25
1963	240,000	54	0.22
1964	390,000	77	0.20
1965	460,000	92	0.20
1966	374,000	58	0.15
1967	257,000	39	0.16
1968	229,000	35	0.15
1969	461,000	68	0.15
1970	467,000	70	0.15
1971	254,000	43	0.17
1972	380,000	61	0.16
1959-72	4,790,000	857	0.18

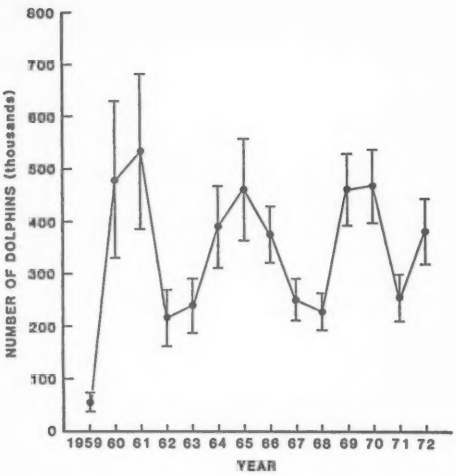

FIGURE 1.—Estimated numbers of dolphins killed in the eastern tropical Pacific tuna purse seine fishery from 1959 to 1972. Standard errors of the estimates shown as vertical bars. From Table 4.

from 32% in 1959 to 15% from 1966 to 1970, and then increase only slightly in 1971 and 1972. The covariances are large (upper triangular matrix, Table 5). They are all positives, and tend to be smaller for pairs of estimates widely spaced in time. The covariances can be examined more easily in terms of correlation coefficients (lower triangular matrix, Table 5). The correlations range from 0.31 to 0.99. The CV of the estimated total is 18%. This is substantially higher than the corresponding value of 6% obtained when the covariances are ignored. Because the total is the sum of 14 numbers, an approximate 95% confidence interval, obtained by adding and subtracting two standard errors, is 3.1-6.5 million dolphins.

The variation in the estimated numbers of dolphins killed over the period 1959-72 is due to several factors: 1) The number of sets made involving dolphins varied from year to year depending on the number of sets of tuna schooling in the absence of dolphins; such tuna are apparently preferred when available. 2) The use of the backdown dolphin-release procedure increased rapidly from 1959 to 1964. However, the development of the backdown dolphin-release procedure is not well known. The available data reflect the tendency of captains to use the technique once it was known. There is little information on how rapidly the procedure became known to other captains and no information on how rapidly they learned to use it effectively. Our assumption of a linear increase probably overestimates the use of backdown initially, but may or may not overestimate its subsequent use. 3) The proportion of successful sets made by small vessels increased from about 50% from 1959 to 1964, to >75% from 1965 to 1972 (Table 1). The higher dolphin kill rate for successful sets results in an increase in estimated dolphin kills as the proportion of successful sets increased. 4) The increase in the proportion of sets which were made by large vessels starting in 1968 results in a decrease in estimated dolphin kill rates due to the lower dolphin kill rate of these vessels.

Several factors which may have affected the numbers of dolphins killed in this period have not been accounted for because of the assumptions made by incomplete data. Chief among these assumptions were 1) the relatively small samples are representative of the fleet as a whole, 2) the kill rates on unsuccessful sets are not affected by the use of backdown, 3) the ratio of kill-per-set in successful sets without backdown to that with backdown is constant

TABLE 5.—Covariances (upper triangular matrix, $x10^{10}$) and correlation coefficients (lower triangular matrix) for the estimated total dolphins killed by year, from 1959 to 1972.

	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972
1959		0.41	0.42	0.14	0.13	0.16	0.15	0.11	0.07	0.06	0.13	0.13	0.06	0.04
1960	0.99		3.49	1.24	1.15	1.37	1.32	0.92	0.62	0.56	1.10	1.08	0.54	0.40
1961	0.99	0.99		1.27	1.19	1.45	1.38	0.95	0.64	0.57	1.13	1.11	0.55	0.42
1962	0.97	0.98	0.99		0.44	0.55	0.52	0.34	0.23	0.21	0.41	0.40	0.19	0.15
1963	0.92	0.94	0.96	0.98		0.58	0.53	0.33	0.22	0.20	0.39	0.38	0.18	0.15
1964	0.76	0.79	0.83	0.88	0.95		0.75	0.43	0.29	0.26	0.50	0.49	0.23	0.20
1965	0.79	0.81	0.84	0.88	0.92	0.93		0.56	0.34	0.27	0.51	0.50	0.23	0.20
1966	0.65	0.66	0.67	0.67	0.67	0.62	0.86		0.30	0.21	0.39	0.38	0.17	0.16
1967	0.75	0.76	0.77	0.78	0.78	0.71	0.89	0.93		0.16	0.30	0.29	0.13	0.10
1968	0.74	0.75	0.76	0.77	0.76	0.70	0.77	0.69	0.90		0.31	0.30	0.14	0.10
1969	0.73	0.74	0.75	0.76	0.75	0.68	0.75	0.66	0.87	0.98		0.63	0.33	0.27
1970	0.71	0.72	0.73	0.73	0.72	0.65	0.70	0.62	0.83	0.94	0.98		0.36	0.38
1971	0.58	0.59	0.59	0.59	0.57	0.50	0.54	0.46	0.63	0.75	0.85	0.92		0.25
1972	0.34	0.35	0.36	0.36	0.36	0.34	0.37	0.34	0.39	0.43	0.55	0.65	0.83	

for both large and small vessels for all years, and 4) the kill rate itself for sets with backdown did not change over the years.

Although each of the unaccounted for factors could have an effect on the estimated numbers of dolphins killed, the magnitude of such effects is probably smaller than the magnitude of the effects of vessel size, set success, and use of backdown described in this study. For example, although the kill rate data available are few, there are some additional data which are not available to us, but which are reportedly similar (Smith and Lo 1983). The last three assumptions noted above deal with the dolphin kill rates with and without backdown, and would tend to both increase and decrease the estimates, if they could be taken into account.

Our estimates of the total number of dolphins killed (Table 4) are slightly lower than previous estimates made using the same method (Smith 1979[6], 1983). The previously estimated total number of dolphins killed from 1959 to 1972 was 5.1 million (total of Smith's [1983] table 4, divided by 0.96 for other species and by 1.048 for injured animals). The difference between the two estimates resulted from the revision of the estimated number of sets that capture tuna associated with dolphins (Punsly 1983) and of the numbers of dolphins killed per set (Smith and Lo 1983).

There are alternate approaches to estimating the numbers of dolphin killed. For example, estimates could be made from data on the numbers of fishing trips made (kill-per-trip), or the number of tons of tuna caught (kill-per-ton). These approaches make different assumptions about the fishing process (Lo et al. 1982; Hammond and Tsai 1983), and require data which are not as precise as are data on the total numbers of sets. For example, fishing trips are difficult to count consistently because they may not be completed within the calendar year and may be extended by partial unloading of the catch. There are fewer such problems with the data for kill-per-set estimators on the number of dolphins killed, and the problems that exist have already been resolved (Punsley 1983).

[6]Smith, T. D. (editor). 1979. Report of the Status of Porpoise Stocks Workshop, August 27-31, 1979, Southwest Fisheries Center, La Jolla, California. Southwest Fish. Cent., Admin. Rep. LJ-79-41, 120 p.

LITERATURE CITED

ANONYMOUS.
1962. How tuna seining paid off for the U.S. fleet in 1961. Fish Boat, Feb., p. 19-30.

BARHAM, E. G., W. K. TAGUCHI, AND S. B. REILLY.
1977. Porpoise rescue methods in the yellowfin purse seine fishery and the importance of Medina panel mesh size. Mar. Fish. Rev. 39(5):1-10.

GREEN, R. E., W. F. PERRIN, AND B. P. PETRICH.
1971. The American tuna purse seine fishery. *In* Hilmar Kristjonsson (editor), Modern Fishing Gear of the World, Vol. 3, p. 182-194. Fish. News (Books) Ltd., Lond.

HAMMOND, P. S., AND K. T. TSAI.
1983. Dolphin mortality incidental to purse-seining for tunas in the eastern Pacific Ocean, 1979-81. Rep. Int. Whaling Comm. 33:589-597.

LO, N. C. H., J. POWERS, AND B. E. WAHLEN.
1982. Estimating and monitoring incidental dolphin mortality in the eastern tropical Pacific tuna purse seine fishery. Fish. Bull., U.S. 80:396-401.

PERRIN, W. F.
1969. Using porpoise to catch tuna. World Fishing 18(6): 42-45.
1969. The problem of porpoise mortality in the U.S. tropical tuna fishery. Proceedings of the 6th Annual Conference on Biology, Sonar, and Diving Mammals, p. 45-48. Stanford Research Institute.

PERRIN, W. F., T. D. SMITH, AND G. T. SAKAGAWA.
1982. Status of populations of spotted dolphin, *Stenella attenuata*, and spinner dolphin, *S. longirostris*, in the eastern tropical Pacific. *In* FAO, Mammals in the seas, Vol. IV. Small cetaceans, seals, sirenians, and otters, p. 67-83.

PUNSLY, R. G.
1983. Estimation of the number of purse-seiner sets on tuna associated with dolphins in the eastern Pacific Ocean during 1959-1980. Inter-Am. Trop. Tuna Comm. Bull. 18:229-299.

SMITH, T. D.
1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. Fish. Bull., U.S. 81:1-14.

SMITH, T. D., AND N. C. H. LO.
1983. Some data on dolphin mortality in the eastern tropical Pacific tuna purse seine fishery prior to 1970. U.S. Dep. Commer., NOAA Tech. Memo. SWFC-TM-NMFS-34, 26 p.

APPENDIX

In Equation (7), the first and second terms on the main diagonal are

$$V(\hat{R}_{\bullet t11} f_t) = V(\hat{R}_{\bullet i11})V(f_t) + \hat{R}^2_{\bullet t11} V(f_t) + f_t^2 V(\hat{R}_{\bullet t11}) \quad \text{(A-1)}$$

for $i = 1$ and 2, noting that $\text{Cov}(\hat{R}_{\bullet t11} f_t) = 0$.
The variance of f_t is given by

$$\begin{aligned} V(f_t) = {} & V(\hat{P}_t)(1 + V(\hat{C})) + \hat{P}_t^2 V(\hat{C}) \\ & + \hat{C}^2 V(\hat{P}_t) + V(\hat{C}) - 2V(\hat{P}_t)\hat{C} \\ & - 2V(\hat{C})\hat{P}_t^2 + 2\,\text{Cov}(\hat{P}_t, \hat{C}). \end{aligned} \quad \text{(A-2)}$$

This last term is assumed to be zero, as noted above. The off-diagonal element in Equation (7) is

$$\text{Cov}(\hat{R}_{\bullet i11} f_t, \hat{R}_{\bullet j11} f_t) \approx \hat{R}_{\bullet i11} \hat{R}_{\bullet j11} V(f_t) \quad \text{(A-3)}$$

for $i \neq j = 1$ and 2.

In Equation (8), based upon Equation (5)

$$\text{Cov}(\hat{Q}_{ui}, \hat{Q}_{mj}) = \begin{cases} \text{Cov}(\hat{R}_{\bullet i11} f_u, \hat{R}_{\bullet j11} f_m) & \text{for } i = 1,2 \text{ and } j = 1,2 \\ 0 \qquad i \neq j & \text{for } i = 3,4 \\ V(\hat{R}_{\bullet i2\bullet}) \qquad i = j & \text{and } j = 3,4 \end{cases}$$

where $\text{Cov}(\hat{R}_{\bullet i11} f_u, \hat{R}_{\bullet j11} f_m)$ (A-4)

$$= \begin{cases} [\hat{R}^2_{\bullet i11} + V(\hat{R}_{\bullet j11})]\text{Cov}(f_u, f_m) + f_u f_m V(\hat{R}_{\bullet i11}) & i = j \\ \hat{R}_{\bullet i11}\hat{R}_{\bullet j11}\,\text{Cov}(f_u, f_m) & i \neq j \end{cases}$$

assuming $\text{Cov}(\hat{R}_{\bullet i11}, \hat{R}_{\bullet j11}) = 0$

$$\begin{aligned} \text{and } \text{Cov}(f_u, f_m) \approx {} & \text{Cov}(\hat{P}_u, \hat{P}_m)[V(\hat{C}) + \hat{C}^2] \\ & + V(\hat{C}) \bullet [1 + \hat{P}_u \hat{P}_m - \hat{P}_u - \hat{P}_m]. \end{aligned} \quad \text{(A-5)}$$

THE ABUNDANCE AND DISTRIBUTION OF THE FAMILY MACROURIDAE (PISCES: GADIFORMES) IN THE NORFOLK CANYON AREA[1]

ROBERT W. MIDDLETON[2] AND JOHN A. MUSICK[3]

ABSTRACT

The Norfolk Canyon off Virginia and the adjacent slope areas were sampled with 13.7 m otter trawls in June 1973, November 1974, September 1975, and January 1976. Trawl depths ranged from 75 to 3,083 m, and 22 species of macrourids were captured during the study. *Coryphaenoides rupestris* demonstrated seasonal movement to shallower water (ca. 750 m) during winter. *Nezumia bairdii*, *N. aequalis*, and *Coryphaenoides carapinus* exhibited a significant positive correlation between head length and depth (r^2 = 0.47, 0.37, and 0.35, respectively). *Nezumia bairdii* apparently spawns in July or August, and reaches an age of about 11 years. New size records were established for *Nezumia aequalis* (64 mm head length (HL)) and *N. bairdii* (66 mm HL). New depth records were established for *Coelorinchus c. carminatus* and *N. aequalis* (884 and 1,109 m, respectively). The known geographic ranges for *Coelorinchus caribbeus*, *C. occa*, *Nezumia cyrano*, *Coryphaenoides colon*, *Hymenocephalus gracilis*, *H. italicus*, *Bathygadus macrops*, *Macrourus berglax*, and *Gadomus dispar* were extended to the Norfolk Canyon area.

The Macrouridae (Pisces: Gadiformes) includes some of the most abundant archibenthic deep-sea fish species (Marshall 1965, 1971; Marshall and Iwamoto 1973; Iwamoto and Stein 1974) and attains greatest abundance and diversity on the continental slopes of the world oceans (Marshall and Iwamoto 1973). Present knowledge of the life history and ecology of macrourids has been accrued piecemeal from faunal lists and taxonomic works (Gunnerus 1765; Gunther 1887; Gilbert and Hubbs 1920; Farron 1924; Iwamoto 1970; Okamura 1970; Marshall and Iwamoto 1973; Iwamoto and Stein 1974), or from studies on physiology, anatomy, and life history (Kulikova 1957; Marshall 1965; Phleger 1971; Rannou 1975; Rannou and Thiriot-Quiereaux 1975; Haedrich and Polloni 1976; McLellan 1977; Merrett 1978; Smith et al. 1979). The meager literature on reproduction and growth of macrourids and other deep-sea anacanthine fishes has recently been reviewed by Gordon (1979). With the advent of increasing expertise in deepwater trawling, some macrourid species, such as *Coryphaenoides rupestris* and *Macrourus berglax*, have become commercially important in the western North Atlantic. Experimental commercial trawling was initiated by the Soviet Union in 1962, and many studies directly related to the commercial fishing of macrourids have been subsequently published by Soviet workers (Podrazhanskaya 1967, 1971; Savvatimskii 1971, 1972; Grigor'ev 1972) and to a lesser extent by Polish researchers (Stanek 1971; Nodzinski and Zukowski 1971).

The present study examines the seasonal distribution and abundance of the macrourid species captured in the Norfolk Canyon area. In addition aspects of age, growth, and reproduction of selected dominant species are also described.

MATERIALS AND METHODS

Gear

The data presented in this paper were obtained on four cruises to Norfolk Canyon and the adjacent open slope to the south (Fig. 1) conducted by the RV *Columbus Iselin* (June 1973) and RV *James M. Gillis* (November 1974, September 1975, January 1976). On all cruises a 13.7 m semiballoon otter trawl with 1.3 cm (stretched) mesh in the cod end liner and 5.1 cm (stretched) mesh in the wings and body was employed. Steel "china V" doors at the end of 22.9 m bridles were used to permit spreading of the net from a single warp (Musick et al. 1975).

[1]Contribution No. 1226 from the Virginia Institute of Marine Science.

[2]Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA 23062; present address: Minerals Management Service, U.S. Department of the Interior, 1951 Kidwell Drive, Vienna, VA 22180.

[3]Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA 23062

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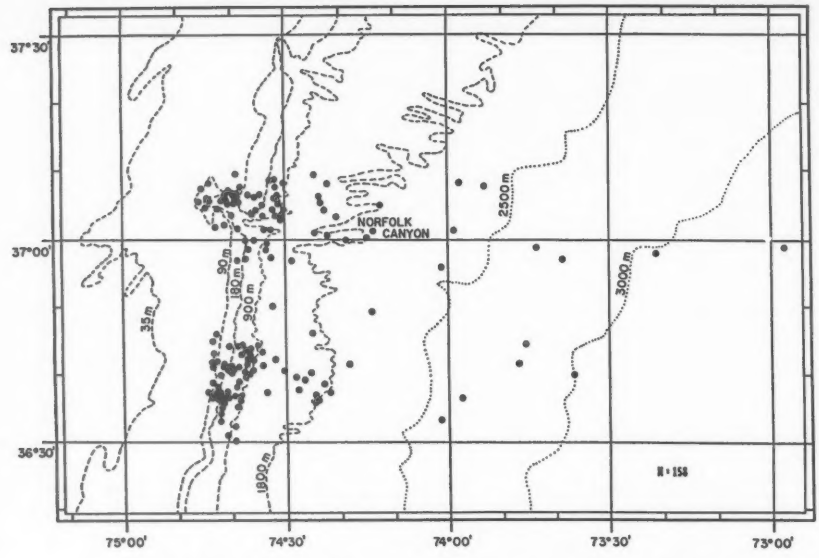


FIGURE 1.—Map of the Norfolk Canyon study area with station locations indicated.

Sampling Design

Norfolk Canyon and an adjacent open slope were divided into five sampling strata: 75-150 m, 151-400 m, 401-1,000 m, 1,001-2,000 m, and 2,001-3,000 m. Six stations were then randomly assigned in each depth stratum. The duration of all tows in depths of <2,000 m was 0.5 h (bottom time). Where the depth exceeded 2,000 m, the tow times were extended to 1 h. Station depth was determined from a sonic precision depth recorder when the net was set and then every 3 min for the duration of the 0.5 h tows (every 6 min for the 1-h tows). Mean station depth was then determined by averaging the 11 resultant values.

Data Collection and Analysis

Head lengths instead of total lengths were measured because macrourids have slender whiplike tails that are easily damaged during trawling. The head length (HL) was measured to the closest millimeter, from the tip of the snout to the posterior edge of the opercle using Helios[4] dial calipers. The fish were weighed with an Ohaus dial-a-gram scale. Calibration showed the scale to be accurate within 1.0-1.5 g under all typical shipboard conditions.

The sex and gonadal conditions of freshly captured specimens were noted. Gonadal samples for histological processing were stored in Davidson's preservative and later mounted using standard paraffin techniques. Sections (5 mm) were stained with Mayer's hematoxylin and eosin counterstain.

Saccular otoliths and a scale sample were removed from all *Nezumia bairdii* and stored dry. Representative otolith samples were chosen randomly from individuals over the entire size range of fish captured.

The length-weight relationships for *Nezumia bairdii*, *Coryphaenoides armatus*, and *C. rupestris* were analyzed using log transformed weights regressed against head length (Fig. 2).

Regression analysis of head length on depth of capture was performed for each species to determine any significant change in head length with change in depth. Testing of the hypothesis that $\beta = 0$ for the regression line ascertained whether there was a significant change of size with changing depth. The coefficient of determination (r^2) was also calculated to determine what proportion of the variance of head length could be attributed to change in depth.

The a posteriori Student-Newman-Keuls analysis of means was used as a second method for interpreting the size/depth relationship. This method calculated the mean depth of capture of each head-

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

length interval, combined the head lengths in subsets whose mean depths did not differ significantly from each other, and defined the constituents of each subset.

Due to the large size and thickness of the macrourid otoliths, standard age determination techniques proved unsuccessful (Christensen 1964; McEachran and Davis 1970). Therefore, a thin section was removed from each otolith and, using a dissecting microscope, the number of bands presumed to be annual were counted and recorded.

Gonads of the specimens were classified into reproductive stages for analysis. The criteria for these stages were as follows:

Stage 1—Undeveloped. The gonads were immature and no development was evident. The reproductive organs were difficult to distinguish within the body cavity.

Stage 2—Early Immature. The reproductive organs had enlarged slightly. The sex could be determined, but no vascularization of the ovaries was apparent. The organs of both sexes had a highly translucent appearance.

Stage 3—Immature. The ovaries were enlarged and vascularization had begun. The testes had become discernibly "sausage shaped". The organs of both sexes were opaque.

Stage 4—Late Immature. The reproductive organs of both sexes were full size. The ovaries were about 90% vascularized. The testes had become milky white in color.

Stage 5—Mature. The reproductive organs were developed completely. Ovaries were fully vascularized and had a granular appearance.

Stage 6—Ripe. Advanced spermatogenesis or oogenesis was evident. The oocytes were fully developed in the females and the male testes contained milky-white seminal fluid.

Stage 7—Spent. The testes and ovaries were spent. The reproductive organs were flaccid and had recently released sperm or eggs.

RESULTS AND DISCUSSION

Species Accounts

Coelorinchus c. carminatus (Goode 1880)

Coelorinchus c. carminatus is a relatively shallow water macrourid reported from depths of 89-849 m (Marshall and Iwamoto 1973). In the study area this species was captured in depths of 210-884 m (Fig. 3). Marshall and Iwamoto (1973) reported *C. c. carminatus* from northern Brazil to the Grand Banks, but absent in the Bahama Island chain. The largest specimen captured in our study had a head length of 70 mm, while Marshall and Iwamoto (1973) reported specimens with 73 mm HL.

During our study, a maximum of 188 individuals and 4 kg of *C. c. carminatus* were captured in a 0.5-h trawl. This species also contributed as much as 34.2% of the number and 27.8% of the biomass of benthic fishes captured in individual samples.

Figure 4 shows the depth distribution of *C. c. carminatus* incremented by 2 mm size groups. A slight increase in head length with increase of depth was apparent. The slopes of the regression lines were shown to be significantly different from zero. The coefficient of determination (Table 1) also showed a correlation between head length and depth. There was variability among cruises, but this may be at-

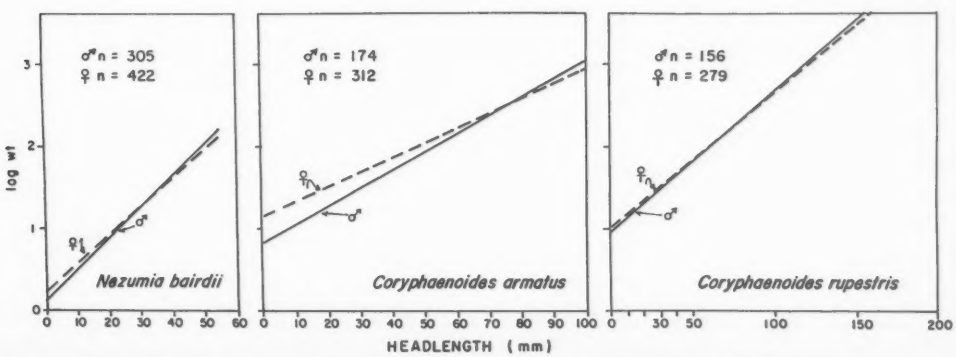


FIGURE 2.—The log (wt) versus head length regressions for *Nezumia bairdii*, *Coryphaenoides armatus*, and *Coryphaenoides rupestris*.

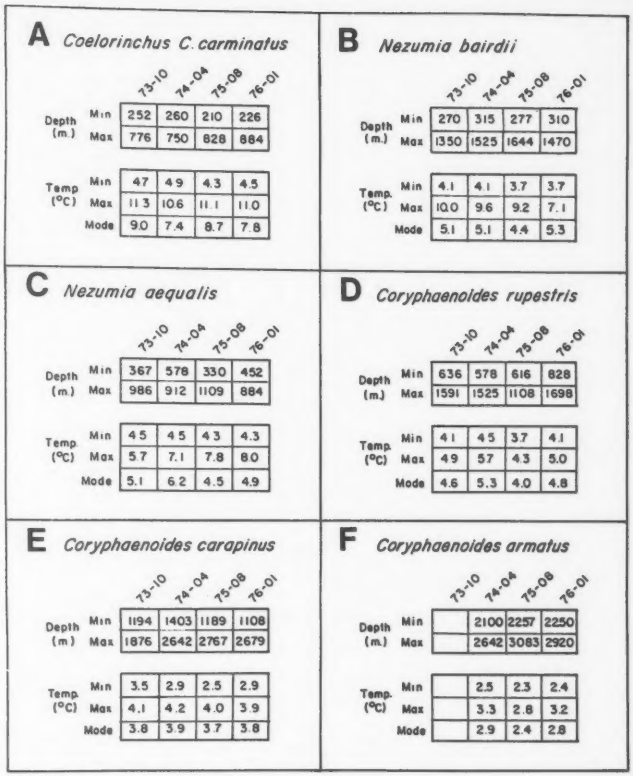


FIGURE 3.—Minimum and maximum depth of capture, with minimum, maximum, and modal temperatures of capture for each species and each cruise.

TABLE 1.—The coefficient of determination (r^2) for the change in head length with change in depth regression lines.

Species	Cruises				Combined cruises
	Jan. 76-01	June 73-10	Sept. 75-08	Nov. 74-04	
Coelorinchus c. carminatus	0.006	0.23	0.13	0.44	0.23
Nezumia aequalis	0.45	0.15	0.62	0.14	0.37
Nezumia bairdii	0.12	0.50	0.44	0.49	0.47
Coryphaenoides rupestris	0.04	0.19	0.08	0.11	0.02
C. carapinus	0.59	0.005	0.30	0.37	0.35
C. armatus	0.000	—	0.05	0.000	0.14

tributed to sampling artifacts and the relatively narrow depth range (674 m) of this species.

The analysis of variance showed a significant difference in mean depths of the head length groups (F = 35.9, F(table; α = 0.01) = 1.79). The Student-Newman-Keuls test divided the group into two significantly different subsets; one 10-50 mm HL and the other 51-70 mm HL.

Other macrourids (*N. bairdii* and *N. aequalis*) had high biomass but low numerical abundance at the deep end of their ranges, indicating the presence of a few large specimens there. This was not the case for *C. c. carminatus* (Fig. 5). The occurrence of fish distributing by size can be obscured if the larger members of the population traverse the entire range. The biomass of the species would be elevated at the shallower depths so that a consistent biomass level is present throughout the depth range. Comparison of Figure 4 with Figure 5 shows that although the mean depth of capture for this species increased with head length, the larger fish occurred over the entire depth range. This pattern is important because it shows that for some fishes the "bigger-deeper" phenomenon described by Polloni et al. (1979) may really be a "smaller-shallower" phenomenon. A plot of mean fish weight against depth as used by Polloni

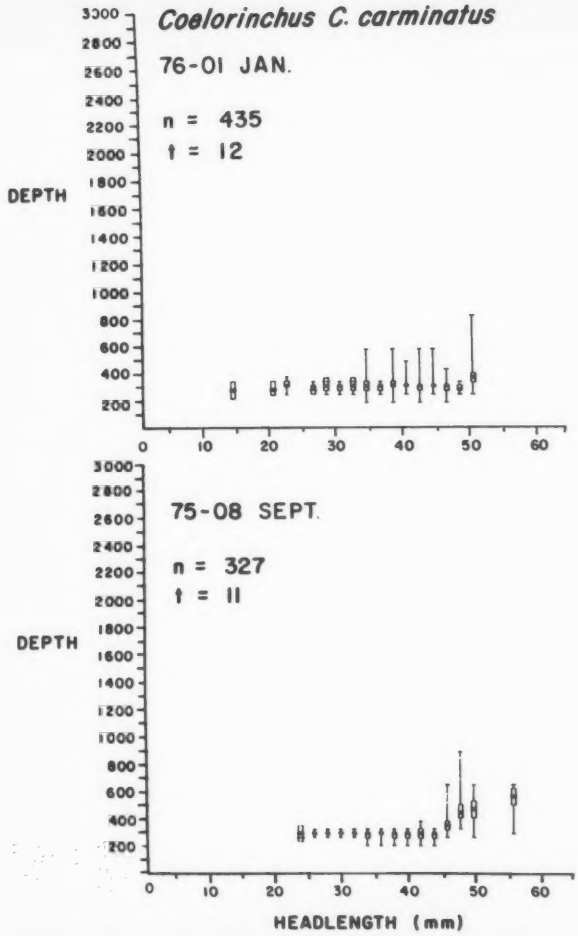
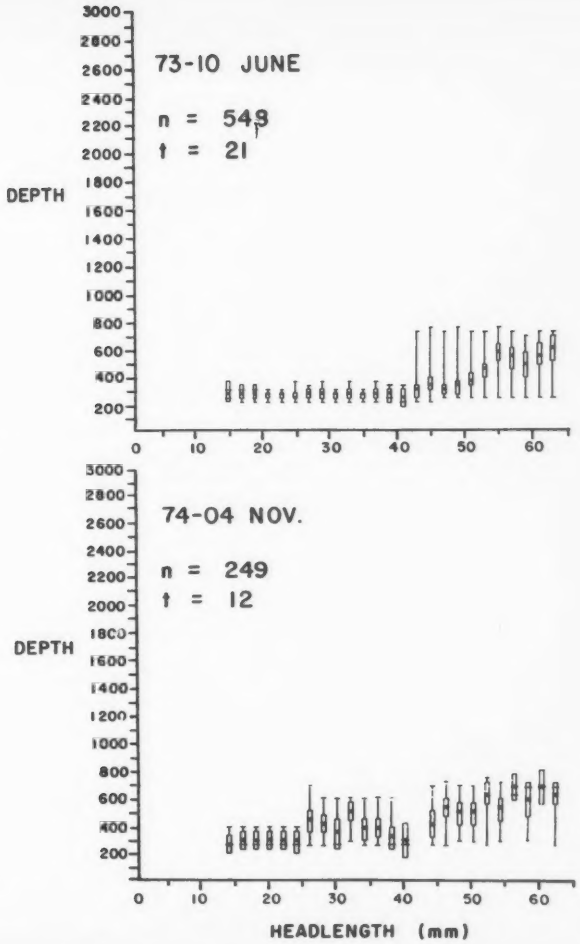


FIGURE 4.—Graph of head length versus depth, by cruise, for *Coelorinchus c. carminatus*. The dot is the mean, the rectangle is the 95% confidence interval, and



the lines each enclose the range. n = the number of specimens and t = the number of trawls.

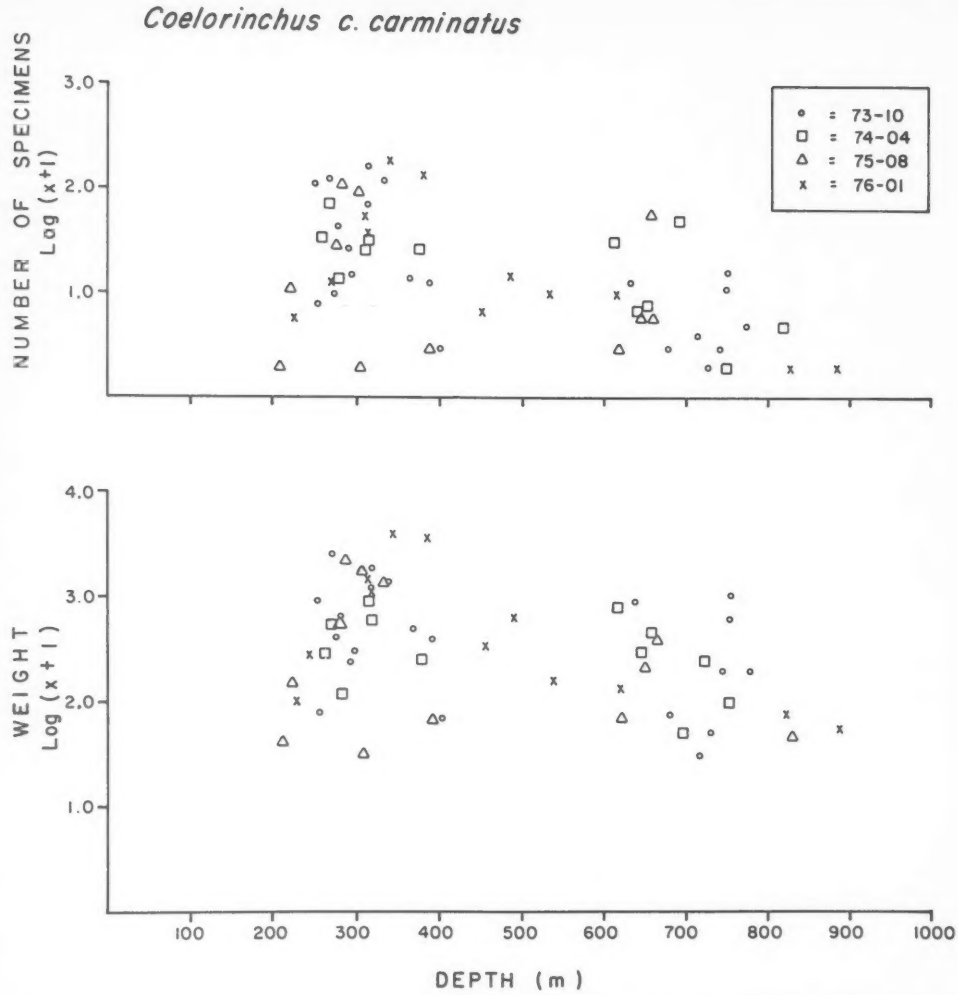


FIGURE 5.—The distribution of log transformed (log (x + 1)) abundance and weight of *Coelorinchus c. carminatus* at each station, plotted against depth.

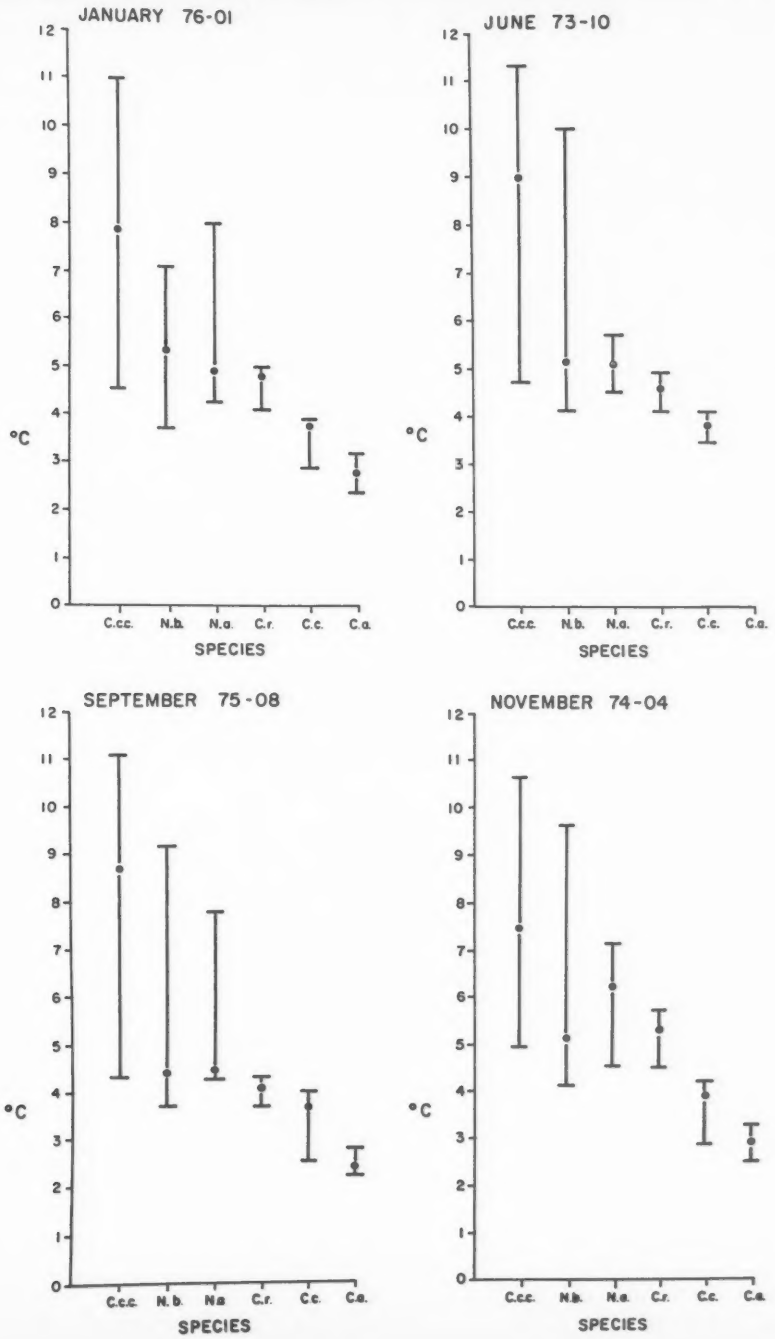
et al. (1979) may have a highly positive slope, but these data are impossible to interpret without information about length-frequency patterns with depth.

The temperatures at which *C. c. carminatus* were captured varied from 4.3° to 11.3°C (Fig. 6). The average temperature of collection was 7.6°C.

***Nezumia aequalis* (Gunther 1878)**

Nezumia aequalis is a closely related congener of *N. bairdii* and is found primarily south of the study area (Marshall and Iwamoto 1973). *Nezumia aequalis* attains a head length of at least 53 mm and has a depth distribution of 200-1,000 m. Its

FIGURE 6.—The temperature range for each species, by cruise. Th dot designates the modal temperature, Ccc. - *Coelorinchus carminatus*, N.b. - *Nezumia bairdii*, N.a. - *Nezumia aequalis*, C. - *Coryphaenoides rupestris*, C.c. - *Coryphaenoides carapinus*, C. - *Coryphaenoides armatus*.


JANUARY 76-01
JUNE 73-10
SEPTEMBER 75-08
NOVEMBER 74-04
°C
0
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8
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12
C.c.c.
N.b.
N.a.
C.r.
C.c.
C.a.
SPECIES

geographic range is listed as from the Faroe bank to northern Angola in the eastern Atlantic, the Mediterranean, and from Davis Straits to northern Brazil in the western Atlantic (Marshall and Iwamoto 1973).

In the Norfolk Canyon area the depth of capture of *N. aequalis* was from 330 to 1,109 m. The greatest number in a trawl was 40 in November of 1974, and the highest biomass per trawl was 300 g in September 1975. *Nezumia aequalis* comprised up to 8.9% of a trawl catch by number and 3.1% by weight. The analysis of variance of the mean depths of the head length groups gave a F value of 3.32 (F(table; α = 0.01) = 2.11). The Student-Newman-Keuls analysis showed only one subset, probably because of the low sample size. Examination of Figure 7 suggests head length increased with depth, and the slope of the line was significantly different from zero.

Although its bathymetric range was extensively sampled, densities were low and few mature specimens were captured (Fig. 8). These findings are in contrast to the distribution and abundance of its cogener, *N. bairdii*, suggesting competitive exclusion. Alternately, Norfolk Canyon populations of *N. aequalis* may represent expatriation from denser populations in the Gulf of Mexico or on the Blake Plateau.

The temperature range for *N. aequalis* captured in the Norfolk Canyon area was from 4.3° to 8.0°C (Fig. 6). The average temperature of collection was 5.3°C.

Nezumia bairdii (Goode and Bean 1877)

Nezumia bairdii is a relatively small macrourid with a reported head length of up to 60 mm (Marshall and Iwamoto 1973). During our study the head lengths varied from 12 to 66 mm with the weight of the largest specimen being 295 g. The geographic range of *N. bairdii* extends from the Straits of Florida north to the Grand Banks (Marshall and Iwamoto 1973). *Nezumia bairdii* is captured commonly between 90 and 183 m in the northern part of its range and appears to undergo tropical submergence because it is found primarily between 548 and 731 m in the southern parts of its range. The inclusive depth range is 90-2,285 m (Goode and Bean 1885; Marshall and Iwamoto 1973). One anomalous catch at a depth of 16.5 m was recorded in Vineyard Sound (Bigelow and Schroeder 1953), but this was most likely a discard from a commercial fishing vessel.

Within the study area the depth of capture ranged from 270 to 1,644 m (Fig. 3). The largest catch in a half hour tow was 76 fish and the greatest biomass per half hour tow was 5.7 kg. *Nezumia bairdii* comprised up to 30% of the demersal fish catch in number and up to 15% of the biomass.

In the January plot (Fig. 9), the head length increased slightly with depth. The regression line of the mean depth of each head length class showed a positive slope significantly different than zero. By June (Fig. 9) the regression line showed a highly significant positive slope and three distinct size groups separated by depth were evident. The first group included those fish <30 mm HL, the second group was from 30 to 42 mm HL, and the third group was >43 mm HL. The head lengths at the start of maturity for females (27 mm) and males (32 mm) correspond well with the dividing line between size groups one and two, as defined by depth distribution. Also, *N. bairdii* females and males can be fully mature at 44 and 45 mm HL, respectively (Fig. 10). These values are close to the division between the second and third size groups noted above. The three size groups appear to reflect maturity stages as well as size differences, and this may contribute to the bathymetric differences. The first group consisted of all immature fish that were not found in deep water in June. The second group could be termed the transitional group because it included fish that were just starting to mature and those more highly developed. Since this group included such a diverse spectrum of maturity, it encompassed portions of the depth ranges of both immature and mature fish. The third group consisted of all mature fish and was not found in water shallower than approximately 600 m in June. In September, the larger fish had reached their deepest limit, and immature *N. bairdii* were virtually absent deeper than 1,000 m. By November (Fig. 9), the largest fish were returning to shallower water to complete what appears to be a seasonal migration cycle.

Examination of histological sections of gonads showed that the only spent *N. bairdii* were captured on the September cruise. Although no ripe fish were caught on any cruise, these spent fish suggest that *N. bairdii* spawns in July or August, coincident with the time when the mature fish are inhabiting their deepest level.

Marshall's (1965) hypothesis concerning reproduction of certain macrourids states that fertilization takes place at the bottom. Subsequently the eggs, which are buoyant, develop and hatch on their way upward to the seasonal thermocline. The larvae then maintain themselves just below the thermocline, in order to take advantage of the plankton that tends to accumulate there in the density gradient. In con-

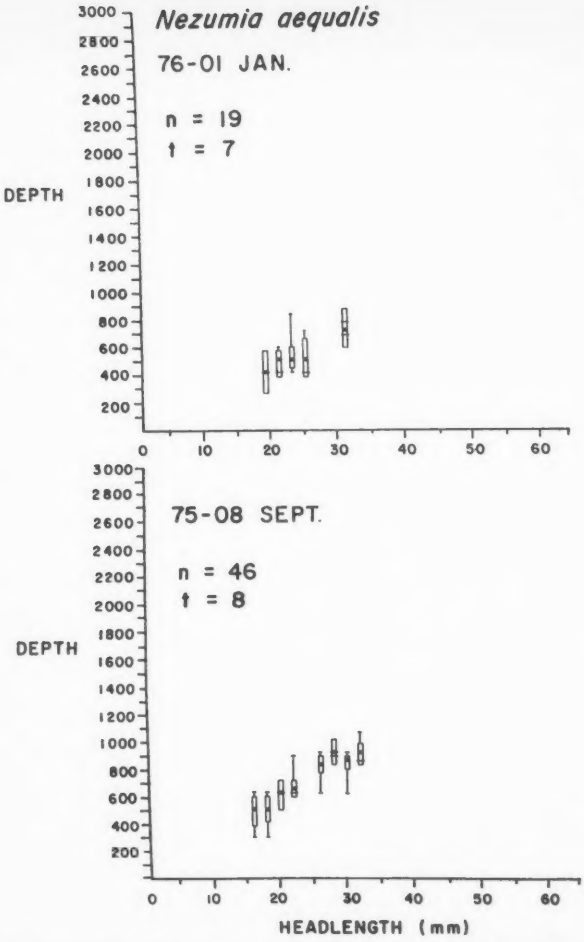
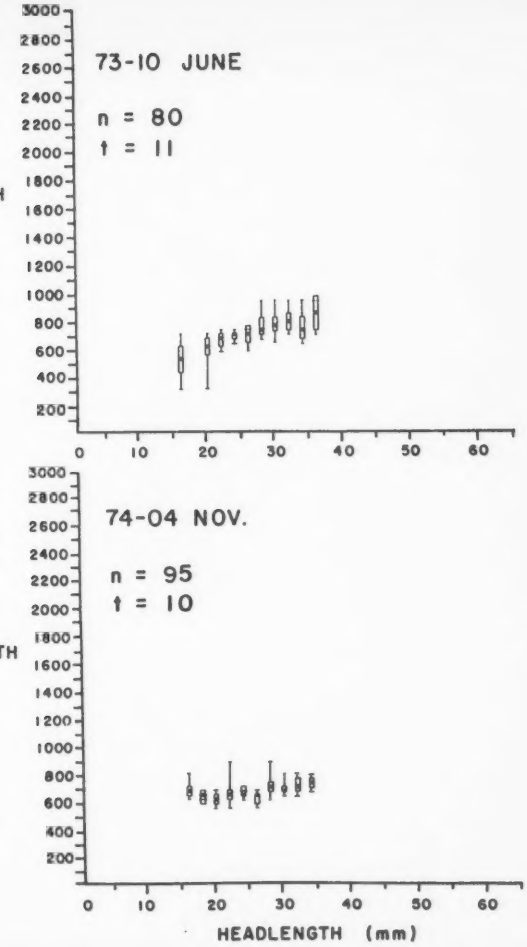


FIGURE 7.—Graph of head length versus depth, by cruise, for *Nezumia aequalis*. The dot is the mean, the rectangle is the 95% confidence interval, and the lines en of trawls.



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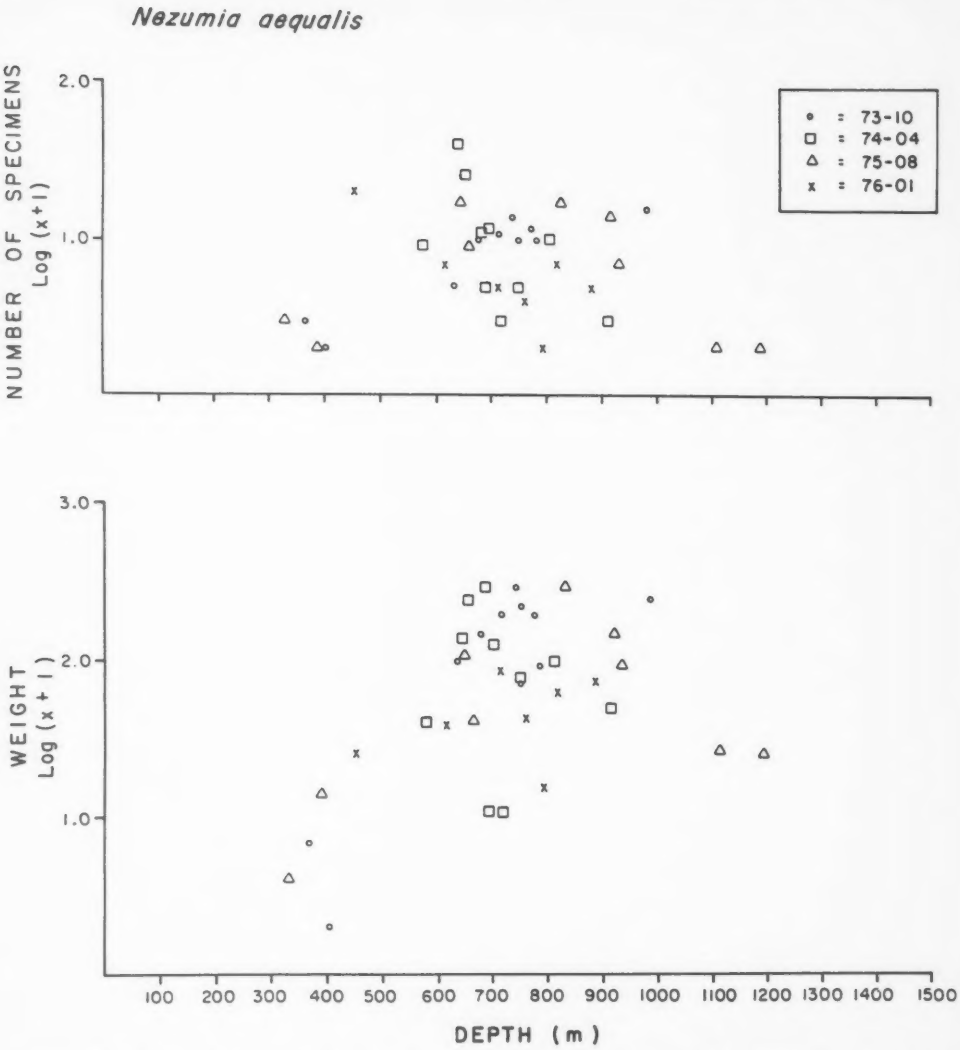

FIGURE 8.—The distribution of log transformed (log (x + 1)) abundance and weight of *Nezumia aequalis* at each station, plotted against depth.

junction with Marshall's hypothesis, the advantages of the type of seasonal migration suggested by our data are twofold. First, the migration concentrates the reproductively mature fish in a limited area thereby increasing the probability of a sexual encounter. Second, it allows additional time for development of eggs on their rise to the upper layers, and concurrently lessens the chance that the egg will travel through the thermocline and be removed from the area by the more active surface currents (although egg density could be such that neutral buoyancy occurs at the thermocline). If these suggestions hold true, it would be expected that the larvae would benefit from the high productivity and warmer temperatures of the surface waters and have enhanced growth. As productivity declines in the late

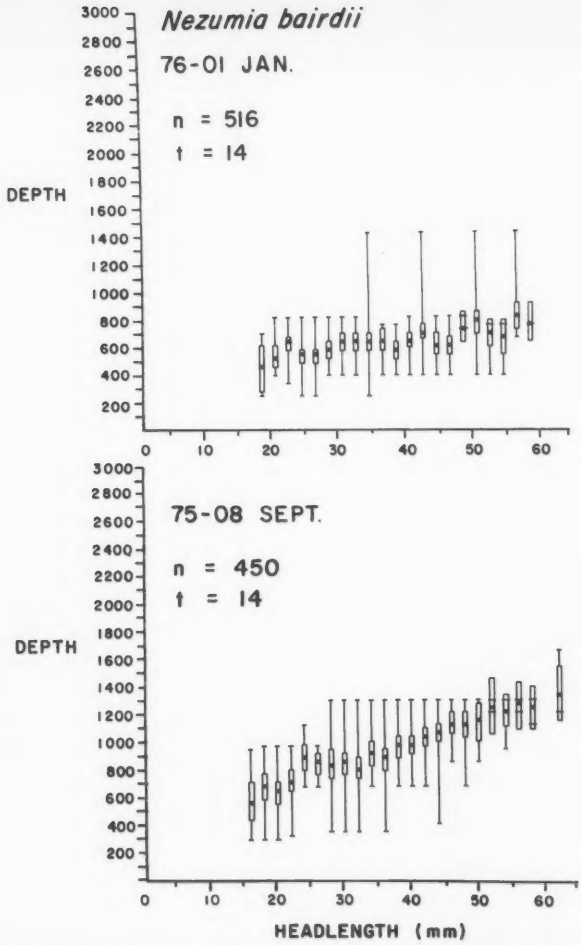

FIGURE 9.—Graph of head length versus depth, by cruise, for *Nezumia bairdii*. T
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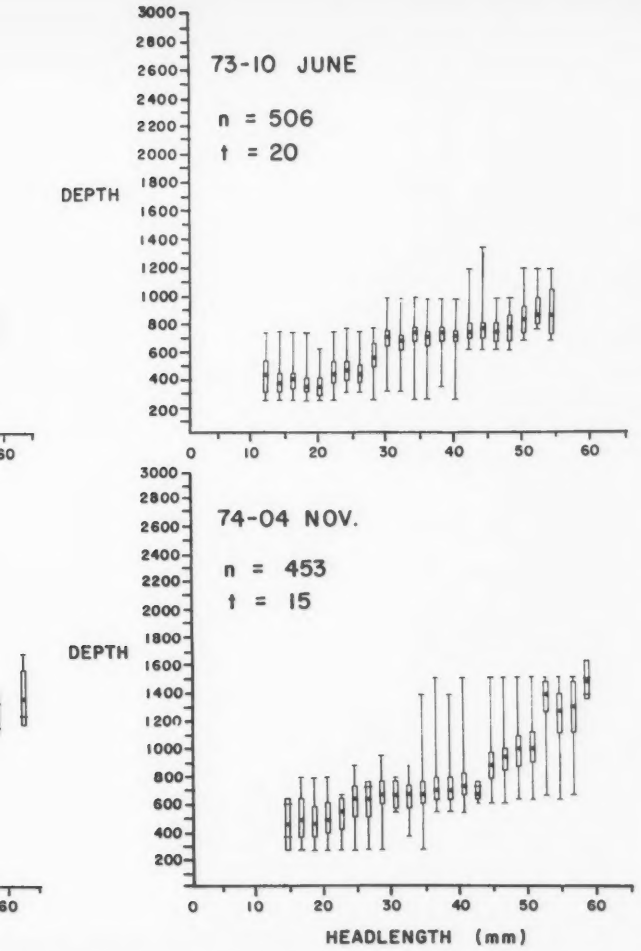


rdii. The dot is the mean, the rectangle is the range. n = the number of specimens and he number of trawls.

fall and the larvae become larger, they would drop out of the water column to the bottom. Length frequencies of *N. bairdii* (Fig. 11) suggested that recruitment of young occurred between the months of November and January. No small *N. bairdii* were captured benthically between the proposed deep-water spawning time and the shallower January recruitment spike.

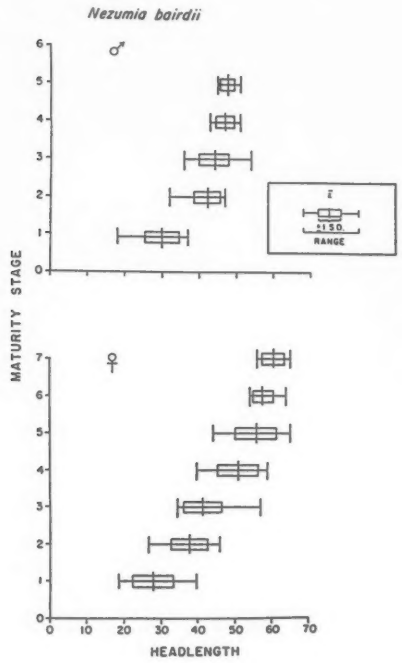


FIGURE 10.—The gonadal maturity stages plotted against head length for *Nezumia bairdii*.

The larger *N. bairdii* occurred deeper than the small ones (Figs. 9, 12) demonstrating the "larger-deeper" phenomenon.

The age and growth analysis of *N. bairdii* presented many problems. Due to the thickness of the sacculus otolith a thin cross section had to be removed from each. After examination of the thin sections, two problems became apparent. First, all of the smaller specimens had two hyaline zones. Because the specimens were obtained on the winter (January; 76-01) cruise, all had hyaline zones around the perimeter as expected. There was, in addition, a well-defined hyaline zone in the interior of all the otoliths obtained from the smallest fishes available (≤27 mm HL). Subsequently two hypotheses were proposed: 1) a period of hyaline zone formation (slow growth) occurred between June-July (spawning) and January, and 2) young *N. bairdii* were not available to our trawl until the second winter hyaline zone was forming (age about 1.5 yr).

The first hypothesis was discarded because a period of slow growth within the first 6 mo would have no apparent selective advantage. It should be noted, however, that since the larvae of *N. bairdii* were probably pelagic, a change from planktonic feeding to benthic feeding would have occurred during that time. Such an ontogenetic change occurs in related gadid fishes. Musick (1969) described the

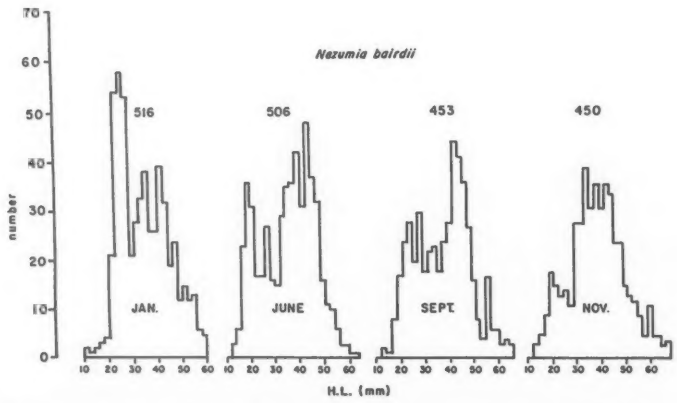


FIGURE 11.—Head length frequency distribution for *Nezumia bairdii* by cruise. The number above each cruise indicates the number of specimens.

ontogenetic transition for *Urophycis chuss* and suggested that the transition from pelagic to demersal adaptations in morphology and behavior occurred within a period of 12-24 h. This short time span would be unlikely to be reflected in macroscopic hyaline band formation. Therefore, the second hypothesis appeared more likely, and led to the conclusion that the juvenile *N. bairdii* remained pelagic until the second winter and then descended from the water column to the bottom where they were captured.

The second problem was that in the older fish (>4 yr) the outer bands were very difficult to define with any degree of confidence. The percentage of unreadable otoliths increased from about 5% in fish ≤4 yr to about 50% in fish >4 yr. The mean head length of *N. bairdii* with four bands was 42.7 mm, the size at the onset of sexual maturity. Growth may have slowed down to compensate for the energy needed for reproduction, and produced spatially close and obscure hyaline zones. Therefore spawning checks may have had considerable influence on

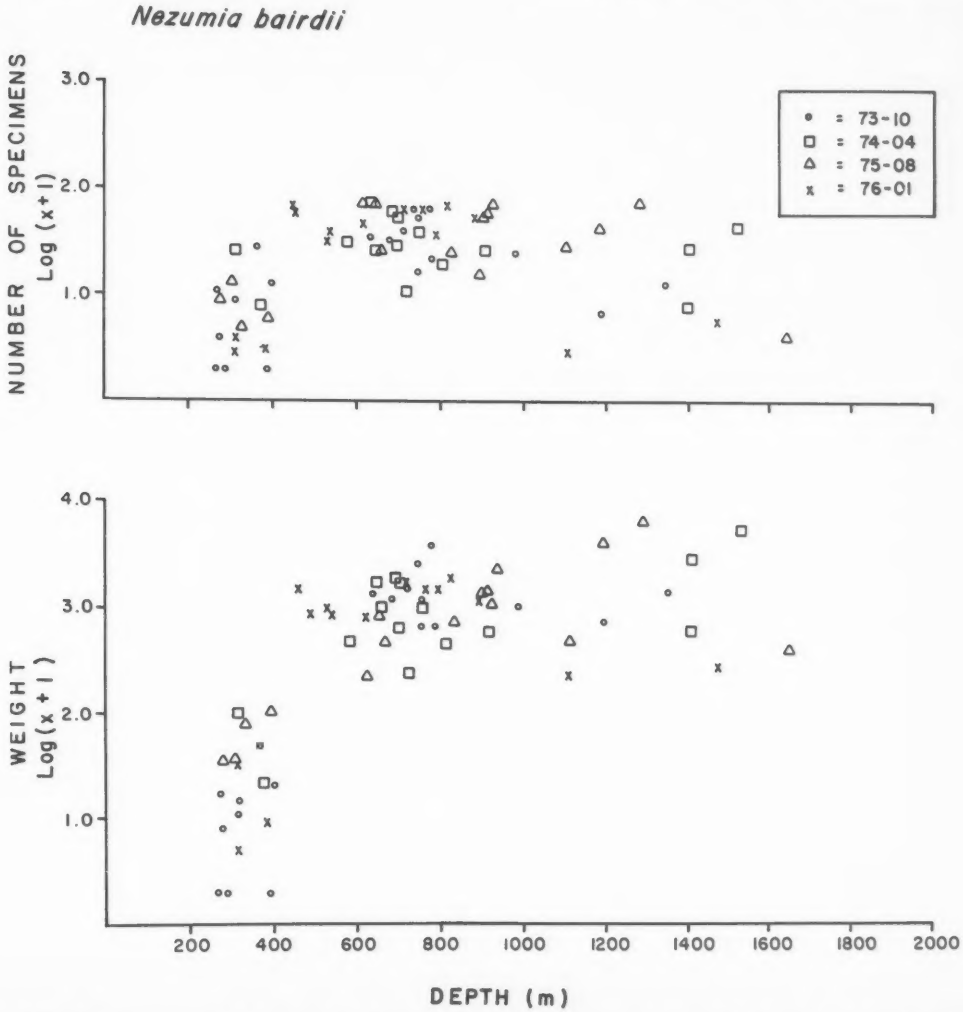


FIGURE 12.–The distribution of log transformed (log (x + 1)) abundance and weight of *Nezumia bairdii* at each station plotted against depth.

the interpretation of the hyaline zones.

Using the length at age data, a Walford growth transformation graph was plotted (Beverton and Holt 1957). Instead of calculating the L_∞, we used our largest specimen (66 mm HL). The estimate of Brody's coefficient (K) obtained from this graph was 0.276. Using the Walford graph, the head lengths for those presumed ages >4 yr could be iteratively generated. This method gave a maximum age of approximately 11 yr. The von Bertalanffy growth equation for length was

$$L_t = 66\ (L - e^{-0.276\ (T+0.16)}).$$

Rannou (1976) studied the age and growth of a congener (*N. sclerorhyncus*) that occupies a similar depth range in the western Mediterranean. He calculated a K coefficient of 0.16 and an L_∞ of 42.31 mm HL. Thus, although this species is smaller than *N. bairdii*, it has a much slower growth rate, probably attributable to lower productivity in the western Mediterranean compared with the slope off the mid-Atlantic coast of the United States (Koblentz-Mishke et al. 1970).

The length-weight regression for *N. bairdii* (Fig. 2) was analyzed. The solution of the line for *N. bairdii* males was log (weight) = 0.038 (head length) + 0.083, r^2 = 0.810, and for females it was log (weight) = 0.035 (head length) + 0.216, r^2 = 0.760.

These length-weight relationships are not unlike those summarized by Gordon (1979) for other small macrourids (*Coelorinchus coelorinchus*, *C. occa*, and *Nezumia aequalis*).

In summary, larger *N. bairdii* were captured deeper and the minimum and maximum depths of capture off the mid-Atlantic coast were 270 m and 1,644 m. The fish seasonally migrated to deeper water with the mature fish occurring deeper than immature fish. The males matured at about 45 mm HL and the females became mature at 44 mm HL. *Nezumia bairdii* probably spawned pelagic eggs in July and August and the young apparently remained pelagic until the second winter (January), when they first appeared in bottom trawls. The maximum age of *N. bairdii* was presumed to be 11 yr. The temperature range for *N. bairdii* was from 3.7° to 10.0°C, with the average temperature of capture being 5.3°C (Fig. 6).

Coryphaenoides rupestris (Gunnerus 1765)

Coryphaenoides rupestris is a large macrourid that reaches a total length of about 100 cm (Savvatimskii 1971; Nodzinski and Zukowski 1971; Marshall and Iwamoto 1973), and is found on both sides of the North Atlantic. In the eastern North Atlantic it ranges from the Trondhjem area to the Bay of Biscay. In the western North Atlantic it is reported to occur from Davis Strait to ca. lat. 37°N (Marshall and Iwamoto 1973), although two specimens (81 and 100 mm HL) were captured by C. Richard Robins[5] at lat. 23°29.8-32.0'N, long. 77°05.5'W. The depth distribution of *C. rupestris* varies from about 180 to 2,200 m (Leim and Scott 1966) with highest abundance occurring between 400 and 1,200 m (Marshall and Iwamoto 1973).

Coryphaenoides rupestris is rarely used as a food fish in the United States, but the German Democratic Republic, the Soviet Union, and Poland fish commercially for it in the western North Atlantic. In 1968, the Soviets recorded a harvest of 30,000 tons of *C. rupestris* off Labrador, Baffin Island, and Greenland (Nodzinksi and Zukowski 1971). The catches of this macrourid were reported to increase during the second half of the year as the catches of redfish and cod decreased (Savvatimskii 1971).

Coryphaenoides rupestris was captured in the Norfolk Canyon area at depths of 578-1,698 m (Fig. 3). Savvatimskii (1971) reported that *C. rupestris* is known to form dense aggregations off the coast of Labrador. In November 1974 an anomalous catch of over 6,000 *C. rupestris* with a total weight >1,000 kg was obtained in a half hour tow in the Norfolk Canyon area. A random subsample of 1,000 specimens was examined and no sexually mature fish were found. Although the head length ranged from 59 to 110 mm, the length-frequency curve was strongly unimodal at 76 mm. The greatest number and biomass of *C. rupestris* caught in "normal" half hour tows was 128 fish comprising 39% of the individuals and 68 kg, and representing 65% of the total catch by weight. The largest specimen captured had a head length of 155 mm.

The head length distribution by depth and by cruise (Fig. 13) suggested a mass movement of *C. rupestris* toward deeper water during the summer months, and a reciprocating movement to shallower water in the winter. In January, the majority of *C. rupestris* was captured between 700 and 800 m, while in June and September there appeared to be a movement toward deeper water. By November the depths of capture decreased and were similar to those of January, and the slope of the head length-depth regression for *C. rupestris* was significantly

[5]C. Richard Robins, Rosenstiel School of Marine and Atmospheric Science, Division of Biology and Living Resources, 4600 Rickenbacker Causeway, Miami, FL 33149.

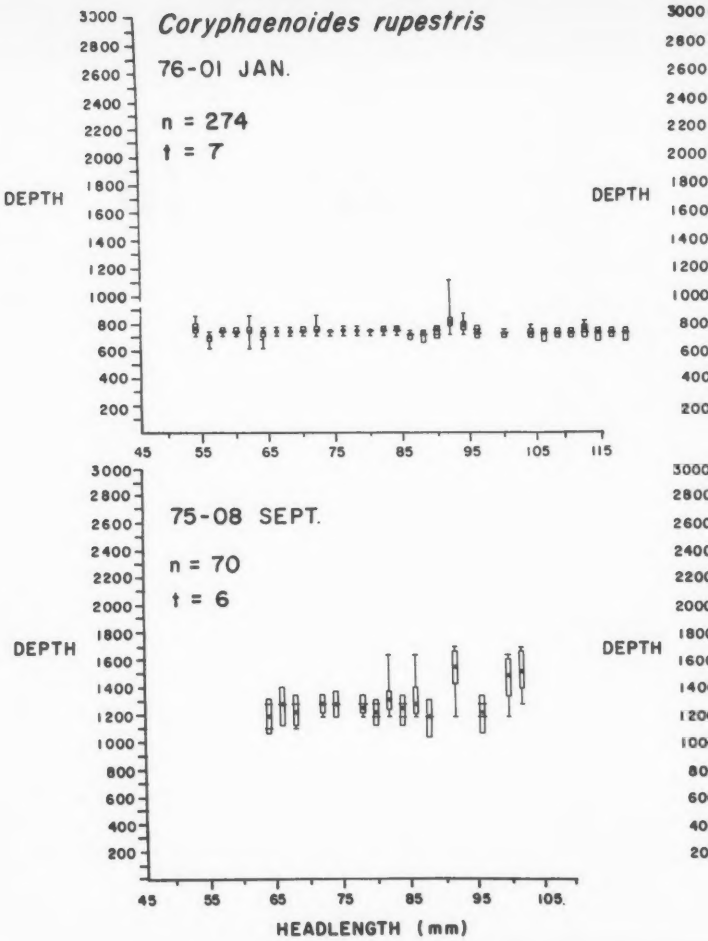
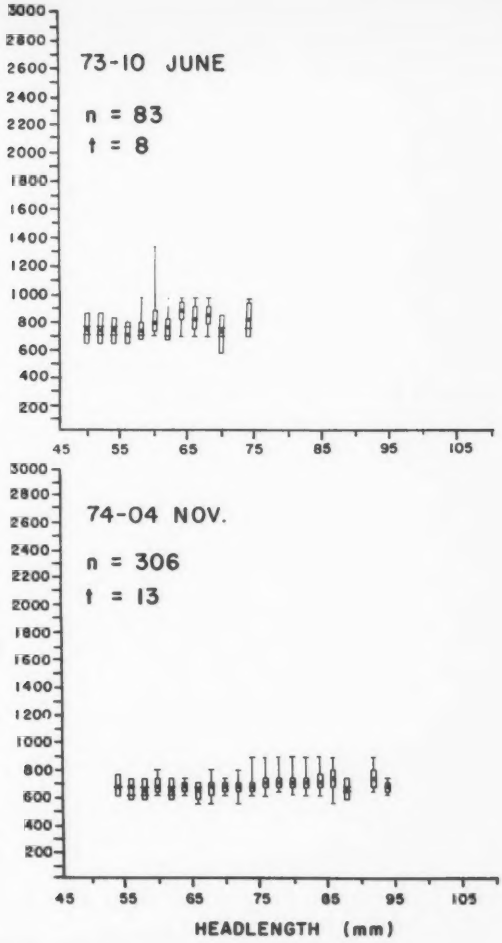


FIGURE 13.—Graph of head length versus depth, by cruise, for *Coryphaenoides rupestris*. The dot is the mean, the rectangle is the 95% cconfidence interval, and the lines e of trawls.



lines enclose the range. n = the number of specimens and t = the number
s.

different from zero. There was no apparent seasonal size segregation evident as in *Nezumia bairdii*, but the graph of numerical abundance against depth also indicated a general seasonal movement down slope in September (Fig. 14). Similar seasonal movements have been shown by Savvatimskii (1971) off Newfoundland.

Females may be mature from about 104 mm HL and males from 71 mm HL (Fig. 15).

Podrazhanskaya (1971) supported Zarkharov and Mokanu's (1970) theory that *C. rupestris* spawns in Icelandic waters. She stated that *C. rupestris* spawn near Iceland and the Irminger Current could transport the eggs and larvae to Greenland. From Greenland the western branch of the West Greenland Current would transport larvae to Baffin Island where the Labrador Current would move the fish down to the Newfoundland banks. When the fish in the Newfoundland area attain a size of 40-50 cm total length (TL), they start to migrate back to Iceland. Podrazhanskaya gave the modal lengths for *C. rupestris* in each area. The smallest fish (modal TL of 45-47 cm) were found on the Northern Newfoundland bank and the largest (modal TL of 98-100 cm) were found around Iceland. Fish from between Baffin Island and West Greenland had modal lengths of 60-62 and 78-80 cm, respectively. Podrazhanskaya's (1971) modal-length data for each area in conjunction with Savvatimskii's (1971) age and growth data reveal that the modal-length fish off the Newfoundland banks are about 6 yr old, off Baffin Island they are 9-10 yr, around Greenland they are 15-16 yr, and at Iceland they are over 20 yr. If a spawning migration occurs, it does not preclude spawning by some members of the population not undergoing migration, thereby accounting for the small percentage of ripening fish to be found outside of their primary spawning area.

If Podrazhanskaya's migration theory is valid, some interesting observations can be made. First, the *C. rupestris* found on the east coast of the United States may be derived from the larvae that failed to metamorphose by the time they reached the Newfoundland banks and continued to drift southwest. The predominant currents move south and west from Newfoundland to Cape Hatteras (Worthington 1964; Webster 1969; Gatien 1976), thereby affording a means of transport for unmetamorphosed larvae (Wenner and Musick 1979). Additionally, the modal length for the 7,011 *C. rupestris* caught in the Nor-

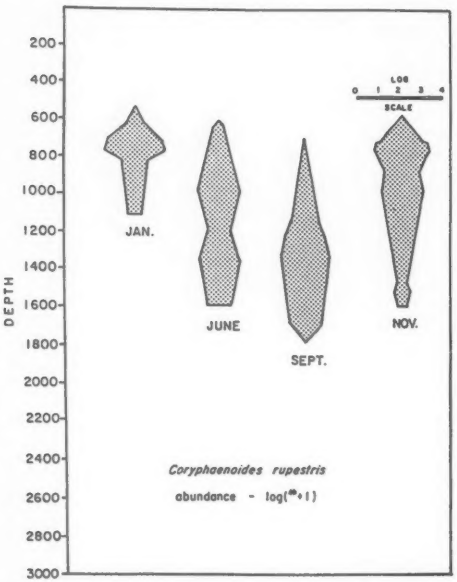


FIGURE 14.—Diagram of depth plotted against the log transformed (log (s + 1)) numerical abundance, by cruise, for *Coryphaenoides rupestris*.

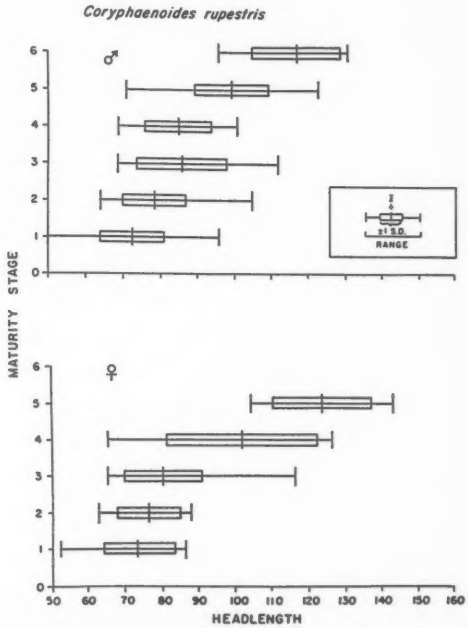


FIGURE 15.—The gonadal maturity stages plotted against head length for *Coryphaenoides rupestris*.

folk Canyon area was 46 cm, exactly that which was found for *C. rupestris* in the Newfoundland bank area. However, no small *C. rupestris* were captured in the Norfolk Canyon area. We found only 2 fish with a head length <40 mm (24 cm TL) and only 10 fish with head length <50 mm (30 cm TL).

The regression line for head length against log (weight) (Fig. 2) was analyzed. The solution for *C. rupestris* males was log (weight) = 0.023 (head length) + 0.82, r^2 = 0.898, and for females it was log (weight) = 0.018 (head length) + 1.16, r^2 = 0.885.

Unfortunately these length-weight data cannot be compared directly with those summarized by Gordon (1979) because we measured head lengths in our study and he gave standard lengths. We do not have the data at present to compute the regression for head length on standard length for this species.

Temperatures at which *C. rupestris* were captured near Norfolk Canyon ranged from 3.7° to 5.7°C (Fig. 6). The average temperature was 4.9°C.

Coryphaenoides rupestris does not follow the "larger-fewer-deeper" pattern shown for *N. bairdii* in Norfolk Canyon because it migrates seasonally (Fig. 16) and the larger specimens traverse the entire bathymetric range (Fig. 13).

In summary, *C. rupestris* migrated seasonally to shallower water in the fall and early winter. Catch per unit effort increased in the fall and winter, and a dense aggregation was found in the fall. Podrazhanskaya's (1971) spawning and migration theory appears feasible but further intensive study is needed. No ripe, running, or spent fish were captured in the Norfolk Canyon area out of 7,011 individuals examined. There was a trend for the larger *C. rupestris* to range deeper but not to the degree that was found in *N. bairdii*. It appears that the distribution of *C. rupestris* was more closely related to temperature than to depth, the species being found mostly within the 4°-5°C range.

Coryphaenoides carapinus (Goode and Bean 1883)

Coryphaenoides carapinus is another small macrourid which grows to about 390 mm TL, and is found on the lower slope and abyss from 1,000 to 3,000 m (Haedrich and Polloni 1976). In the western North Atlantic it has been found between Nova Scotia and Cape Hatteras (lat 37°N) and in the eastern Atlantic from lat. 50°N to the Equator. *Coryphaenoides carapinus* has also been reported from the mid-Atlantic ridge (Marshall and Iwamoto 1973).

In the Norfolk Canyon area *C. carapinus* was captured at 1,108-2,767 m (Fig. 3). The largest number caught in one trawl was 37 (total weight 550 g). These were captured in September 1975 at a depth of 1,803 m. *Coryphaenoides carapinus* comprised up to 23.4% of a catch in number, but only 4.3% in biomass. The maximum size captured was 90 mm HL.

Coryphaenoides carapinus tended to be larger at the lower end of its depth range (Fig. 17). The slope of the regression line for head length with depth was significantly different than zero. The coefficient of determination was 0.346.

Figure 18 displays low numbers and high variability in the capture of *C. carapinus* in relation to depth. The phenomenon of fewer, larger fish at the deeper part of the bathymetric range was evident but obscured because of the relatively small size of *C. carapinus*, low numbers, and contagious distribution.

Coryphaenoides carapinus was taken at temperatures of 2.5°4.2°C with the average temperature being 3.7°C (Fig. 6). Some overlap in distribution with depth and temperature occurred among *C. carapinus*, *C. armatus*, and *C. rupestris*. Because *C. carapinus* is a small species and mostly a benthic feeder (Haedrich and Polloni 1976) and *C. armatus* and *C. rupestris* are large species that forage into the water column (Podrazhanskaya 1971; Haedrich and Henderson 1974; Smith et al. 1979), competitive interaction is probably low.

Coryphaenoides armatus (Hector 1875)

Coryphaenoides armatus is cosmopolitan in distribution, being found in all oceans except the Arctic. It commonly is found from 2,200 to 4,700 m, with a few specimens being captured as shallow as 282 m (Marshall and Iwamoto 1973). Larger individuals have been shown to forage off the bottom for pelagic prey (Haedrich and Henderson 1974; Pearcy 1975; Smith et al. 1979). *Coryphaenoides armatus* attains a size of 165 mm HL and over 870 mm TL (Iwamoto and Stein 1974). The largest specimen captured in Norfolk Canyon was 146 mm HL. Although *C. armatus* is one of the deepest living macrourids, it is rather well-known biologically because of its broad distribution and availability to deepwater trawls (Haedrich and Henderson 1974; Pearcy and Ambler 1974; McLellan 1977; Smith 1978).

Coryphaenoides armatus was taken in every successful trawl from 2,100 m to our deepest trawl of 3,083 m in the Norfolk Canyon area and virtually was confined to below the 3°C isotherm (Fig. 3). In

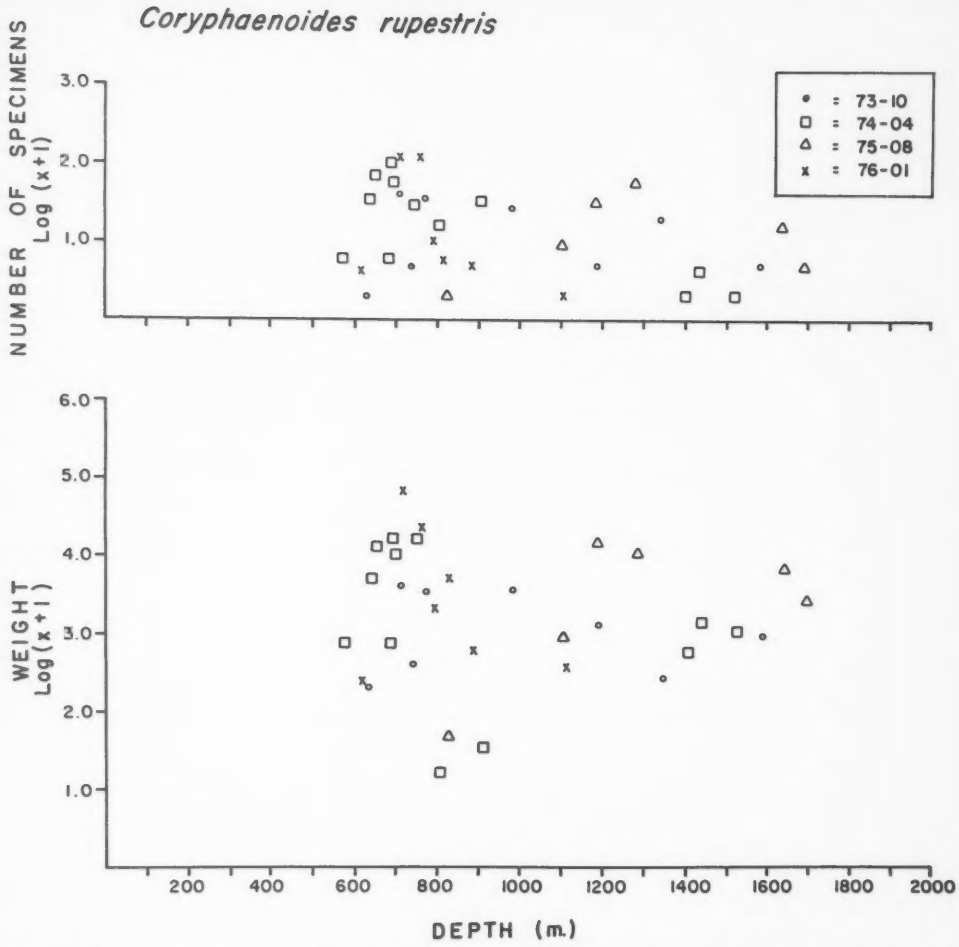


FIGURE 16.—The distribution of log transformed (log (x + 1)) abundance and weight of *Coryphaenoides rupestris* at each station, plotted against depth.

one trawl *C. armatus* comprised 92.7% of the benthopelagic fish numbers and 93.4% of the biomass. In a 1-h trawl the maximum number captured was 76 and the maximum biomass was 21.2 kg.

No increase in fish size with increased depth was evident in the data (Fig. 19) (Table 1), and the slope of the regression line for head length with depth was not significantly different from zero. However, known depth range of *C. armatus* was incompletely sampled in this study, and further samples from greater depth may lead to other conclusions.

The distribution of numerical abundance and weight with depth are shown in Figure 20. *Coryphaenoides armatus* increased in abundance from 2,100 to 2,600 m, beyond which its abundance remained constant.

The regression lines for head length against log (weight) were analyzed (Fig. 2). The solution for males was log (weight) = 0.017 (head length) + 0.956, r^2 = 0.967, and for females it was log (weight) = 0.016 (head length) + 1.029, r^2 = 0.972.

The maturity stages of *C. armatus* against head

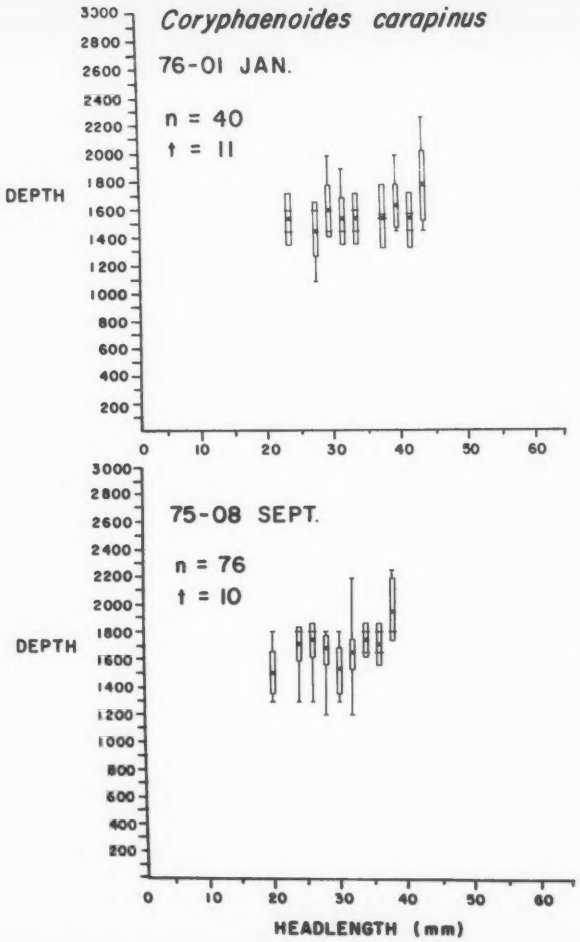
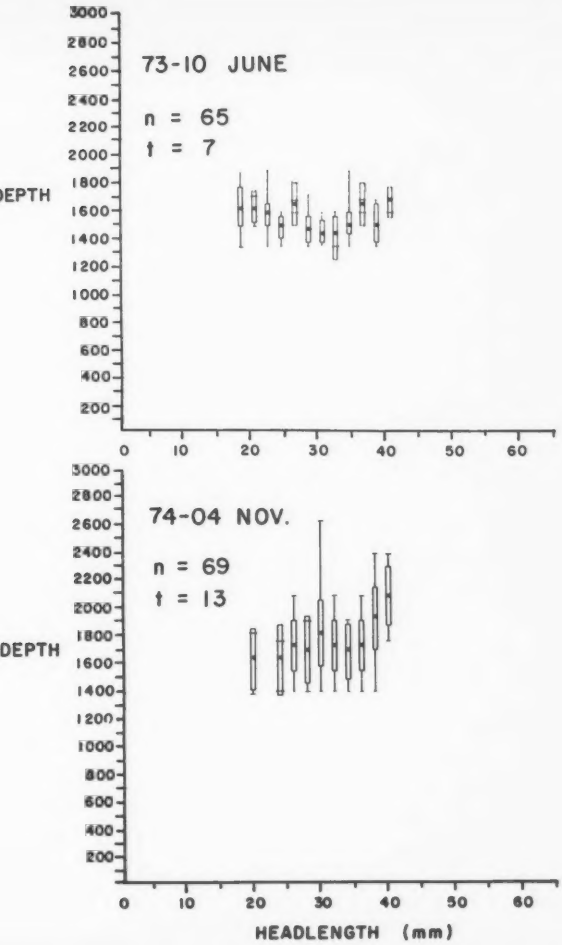


FIGURE 17.—Graph of head length versus depth, by cruise, for *Coryphaenoides carapinus*. The dot is the mean, the rectangle is the 95% confidence interval,



and the lines enclose the range. n = the number of specimens and t = the number of trawls.

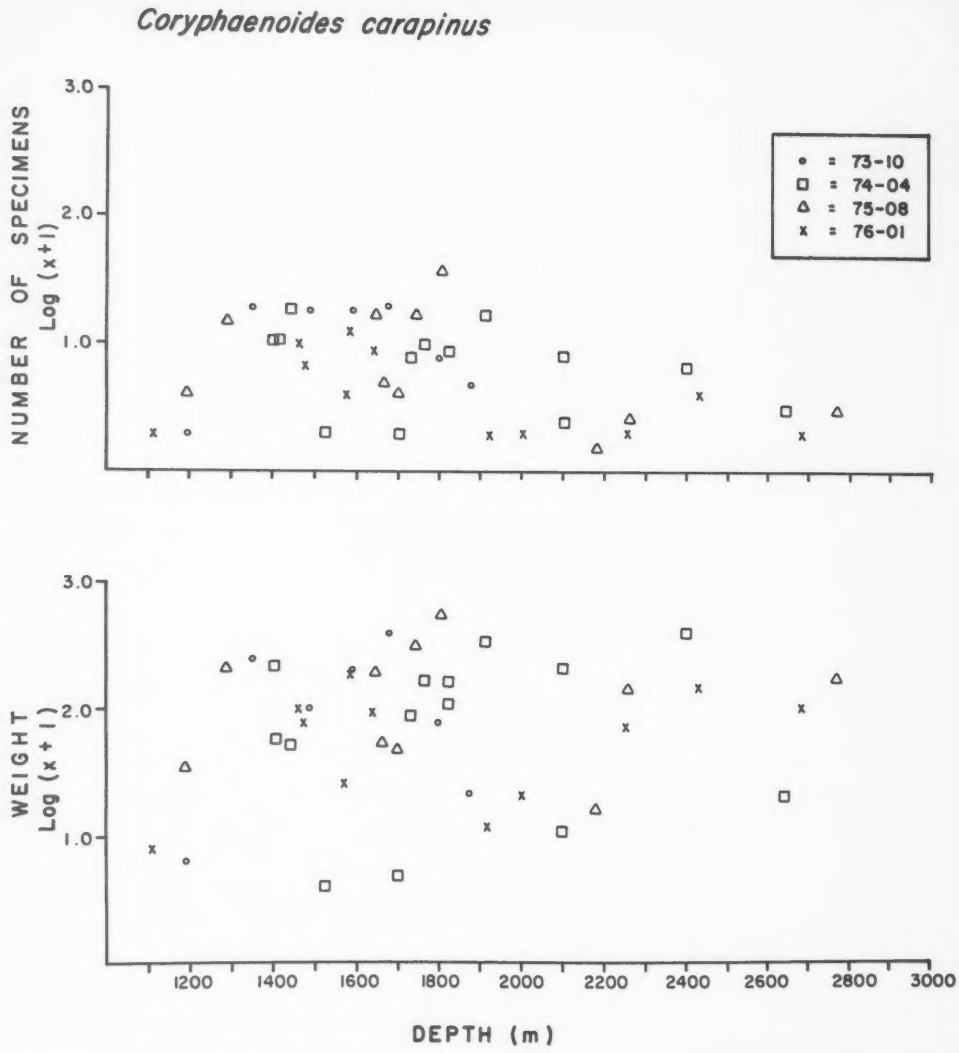


FIGURE 18.—The distribution of log transformed (log (x + 1)) abundance and weight of *Coryphaenoides carapinus* at each station plotted against depth.

lengths are shown in Figure 21. No mature males were found, but the females matured at about 78 mm HL. *Coryphaenoides armatus* was captured in temperatures ranging from 2.3° to 3.3°C (Fig. 6). The majority of individuals, however, were caught between 2.4° and 2.9°C during the study and the average temperature was 2.6°C.

Distribution of Macrourids With Temperature

Depth distribution has been used commonly throughout the literature to delineate the habitat of various fishes, including macrourids (Macpherson 1981). The temperature ranges for each species in

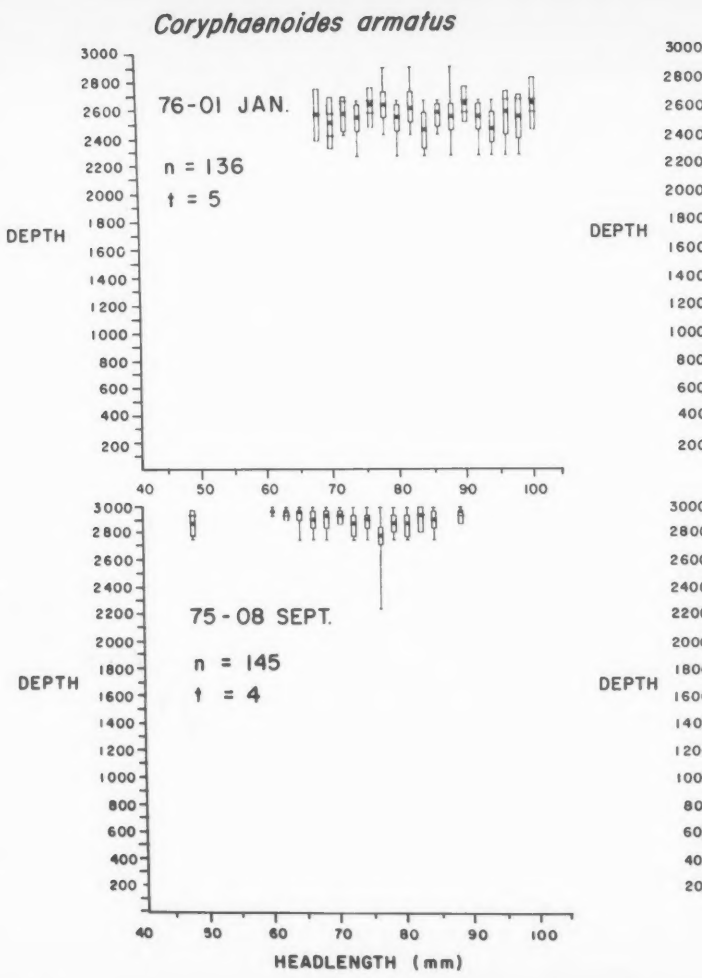
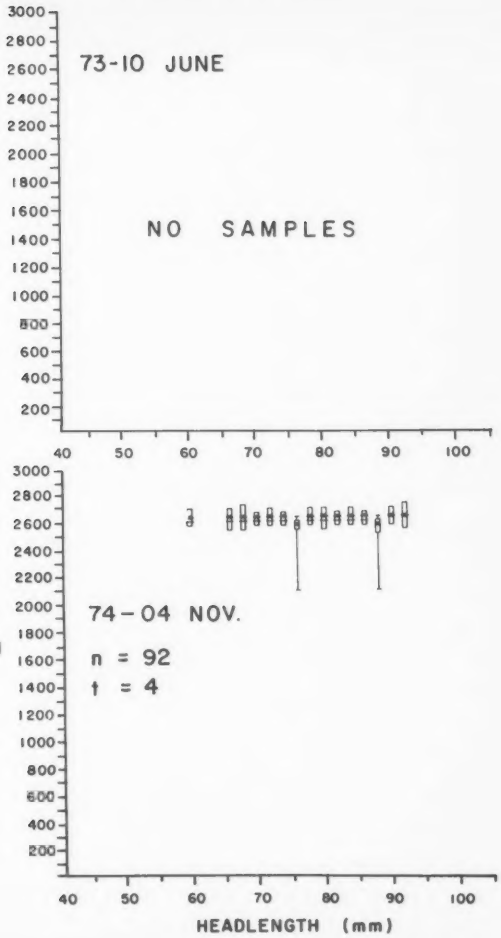


FIGURE 19.—Graph of head length versus depth, by cruise, for *Coryphaenoides armatus*. The dot is the mean, the rectangle is the 95% confidence interval, and the lines enclos of trawls.



enclose the range. n = the number of specimens and t = the number

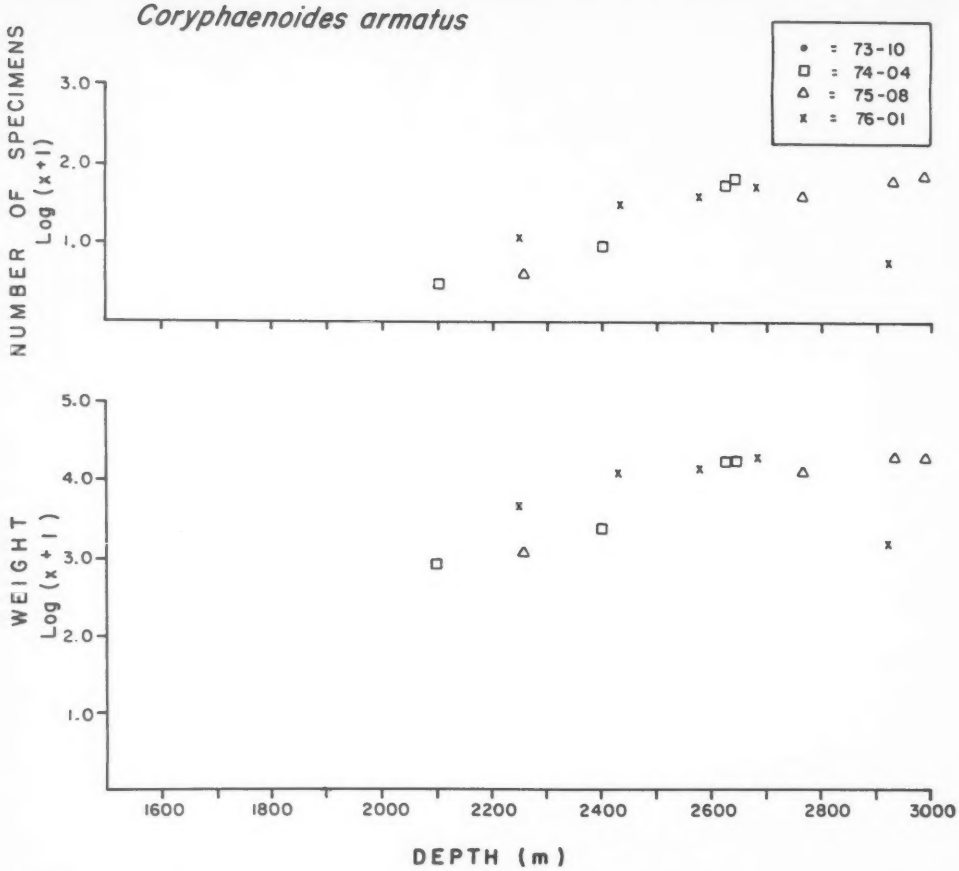


FIGURE 20.—The distribution of log transformed (log (x+1)) abundance and weight of *Coryphaenoides armatus* at each station plotted against depth.

the present study showed some overlap, but the temperatures at which the population modes were found were fairly discrete except for *Nezumia aequalis*, *Nezumia bairdii*, and *Coryphaenoides rupestris*.

In Figure 6 the relationship of species with temperature is more clearly defined. The minimum temperature of each species remained fairly constant as did the maximum and modal temperature for those species in which there was no indication of seasonal migratory patterns (*Coelorinchus carminatus*, *Coryphaenoides carapinus*, *C. armatus*). The 3.5°C minimum temperature found for *C. carapinus* in June was probably not accurate since the deepest trawl of that cruise did not encompass the entire range of *C. carapinus*. Similarly, the minimal temperatures for *C. armatus* may not be representative.

Competition Among Macrourids

Competition among macrourids in the Norfolk Canyon region is probably minimal because the species differ in body size and feeding strategies or, if feeding strategies are similar, the species have different distributions with temperature and depth. Close congeners such as *Nezumia bairdii* and *N. aequalis* might be expected to occupy similar depth

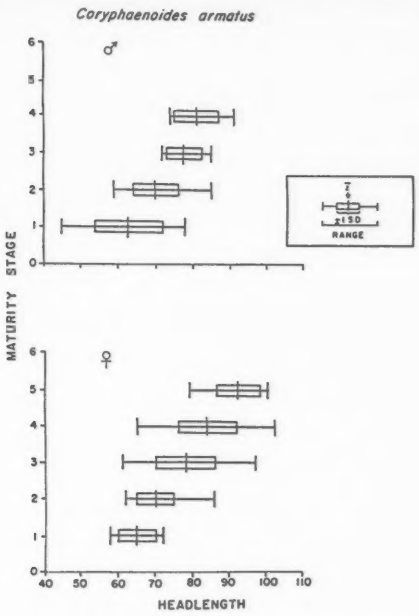


FIGURE 21.–The gonadal maturity stages plotted against head length for *Coryphaenoides armatus*.

and temperature ranges; however, the *N. aequalis* in this area were at the northern limit of their geographic range, occurred in small numbers, and may have been in direct competition with *N. bairdii*. Although *C. rupestris* also occupied the lower section of the two *Nezumia* spp. temperature and depth regimes, direct competition was probably low because of their dissimilarity in mouth size and morphology and related differences in diet (Podrazhanskaya 1971; Geistdoerfer 1975; McLellan 1977).

Abundance and Density of the Family Macrouridae

In the study area the abundance of macrourids, in water shallower than 2,000 m, was fairly constant with respect to other bottom fishes. The average percent of macrourids by number in each cruise was 16.6% in cruise 73-10 (June), 15.0% in 74-04 (December), 14.6% in 75-08 (September), and 18% in 76-01 (January). The major peaks of abundance were found between 300 and 400 m, where *Coelorinchus c. carminatus* was present, and around 800 m where the complex comprised of *Nezumia aequalis*, *N. bairdii*, and *Coryphaenoides rupestris* dominated (Fig. 22). In depths of over 2,000 m the numerical dominance of *C. armatus* was evident. Some of the minor inflections can be attributed to the contagious distributions displayed by these fishes.

The graph of macrourid biomass (Fig. 23), as percent of the catch, was similar to that for numerical abundance except for a shift in biomass from 800 m to below 1,000 m between January and June. This was probably because of the seasonal movement of the larger macrourid *Coryphaenoides rupestris*. Between about 1,400 and 2,200 m, macrourids made up a very small portion of the biomass, although their percent by number was comparable with lesser depths. The dominant macrourid in this area, *C. carapinus*, was small, and *Antimora rostrata*, a large morid, was the most abundant member of the benthic fish community from 1,300 to 2,500 m (Wenner and Musick 1977). In depths >2,200 m the biomass of *C. armatus* steeply increased with depth, until it was the predominant member of the benthic community.

All the macrourid species, with the exception of *C. rupestris*, maintained a fairly constant numerical distribution from cruise to cruise. There was apparent variability for *C. carapinus* and *C. armatus*, but this was due to the small number of samples from deeper areas. Distribution of macrourids as the percent of catch revealed a gradual replacement of species with depth, and the predominance of *C. armatus* in depths >2,500 m.

Macrourids made up a major numerical portion of the benthic fish community from 300 m to the deepest station at 3,083 m. Macrourids were also a main component of the biomass of the communities from 300 to 3,083 m, excluding the 1,300-2,500 m range where the morid, *A. rostrata*, dominated.

Although Macrouridae is a dominant family in the Norfolk Canyon area, the potential for a fishery is essentially nonexistent. *Coryphaenoides rupestris* is the only species which attains an appreciable size in the mid-Atlantic area; a modal length of 46 cm TL. However, this size is much smaller than typically found in the North Atlantic and the density of organisms is generally low (normally <0.86 individuals/100^2). In addition, *C. rupestris* demonstrates a tropical submergence, being found deeper in lower latitudes. The depth range of this species in the Norfolk Canyon area (578-1,698 m), combined with smaller size and lower density of organisms, indicate that a commercial fishery would not be economically feasible.

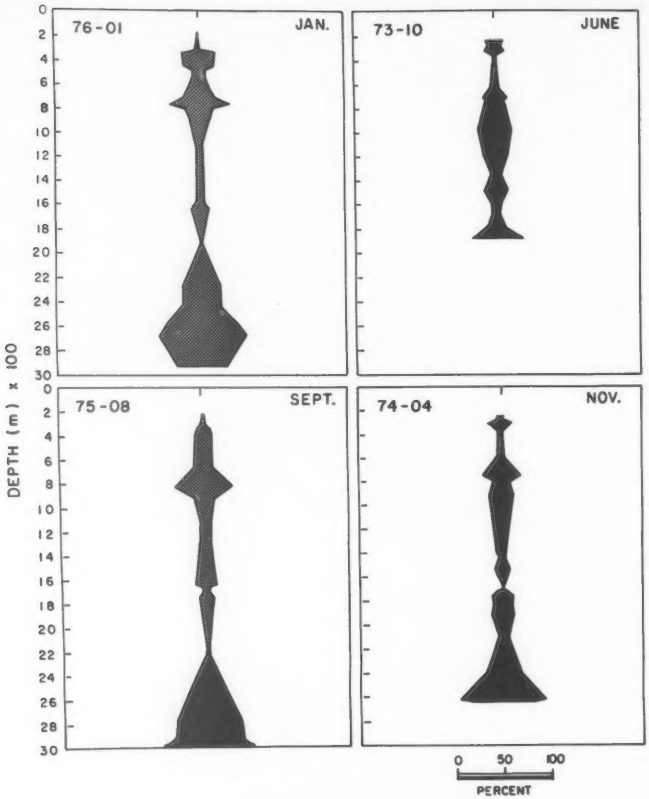


FIGURE 22.—Depth versus relative abundance (as percent, by number, of total capture) for the family Macrouridae, by individual cruise.

Comparison With Other Studies

The comparison of this study with others in the North Atlantic lends support to Marshall and Iwamoto's (1973) hypothesis that the greatest diversity of macrourids is in the bathyal tropical regions. The number of macrourid species declines from tropical to boreal regions. Marshall and Iwamoto (1973) reported 32 macrourid species from the Caribbean and Gulf of Mexico, but only 22 species were captured during our study (Table 2). Bullis and Struhsaker (1970) found that Macrouridae was one of the dominant families on the western Caribbean slope between 201 and 400 fathoms (368-732 m). The deepest stratum sampled was 451-500 fathoms (825-914 m), and macrourids (9 species) comprised about 67% of the individuals captured within these depths. Within the same depths in the Norfolk Canyon area the dominant macrourids (4 species) contributed about 31% to the total catch.

Merrett and Marshall (1981) remarked on the high diversity (and apparent resource partitioning) of macrourids from a tropical upwelling area off northwest Africa and reported 26 species from there. They found 18 species on the slope (≤1,600 m), including four species of *Nezumia*. Bathygadine macrourids were important off Africa but virtually absent in our study area. Thus macrourid diversity is probably highest on the continental slope in the tropics, particularly in areas of higher productivity. In addition, high diversity is manifested there at several taxonomic levels, from the species to the subfamily.

Haedrich et al. (1975) reported the capture of 121 macrourid specimens (3 species) in 29 trawls off Southern New England. Their trawl depths ranged from 141 to 1,928 m. Their findings were similar to

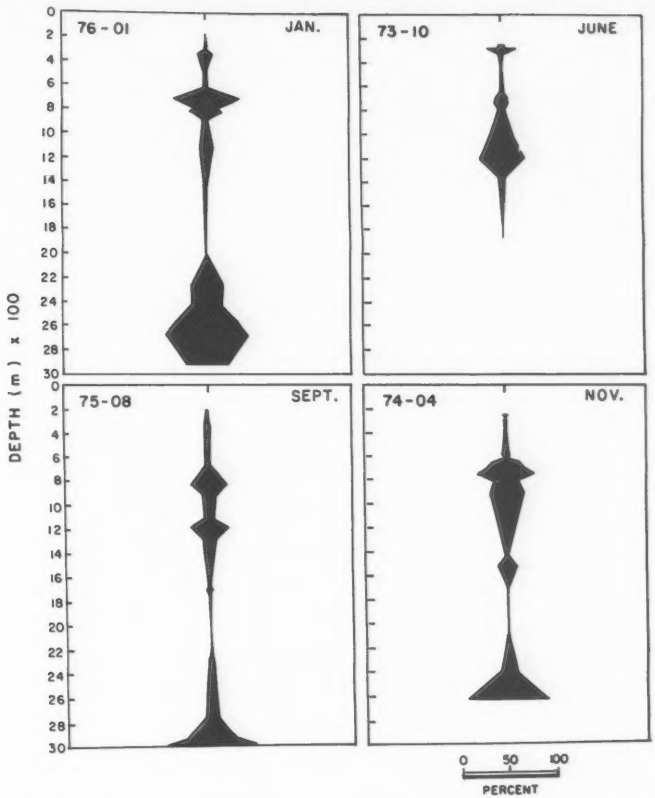


FIGURE 23.—Depth versus relative abundance (as percent, by biomass, of total capture) for the family Macrouridae, by individual cruise.

TABLE 2.—Species captured during study, with total number and total weight.

Species	Total number	Total weight (g)	Species	Total number	Total weight (g)
Coelorinchus c. carminatus	1,827	38,597	*Coryphaenoides colon*[1]	1	20
Coelorinchus caribbaeus[1]	10	419	*Coryphaenoides leptolepis*	12	4,922
Coelorinchus occa[1]	1	2	*Ventrifossa occidentalis*	60	1,449
Nezumia aequalis	285	4,041	*Ventrifossa macropogon*	1	8
Nezumia bairdii	2,222	72,865	*Hymenocephalus gracilis*[1]	1	1
Nezumia longebarbatus[2]	12	1,299	*Hymenocephalus italicus*[1]	1	12
Nezumia sclerorhyncus	1	8	*Bathygadus favosus*	2	—
Nezumia cyrano[1]	1	—	*Bathygadus macrops*[1]	1	22
Coryphaenoides rupestris	7,120	1,229,304	*Sphagemacrurus grenadae*[2]	4	30
Coryphaenoides carapinus	213	4,703	*Macrourus bergiax*[3]	2	4,470
Coryphaenoides armatus	391	120,456	*Gadomus dispar*[1]	1	—

[1]Range extension from the Gulf of Mexico-Caribbean area.
[2]Also reported by Haedrich and Polloni (1974).
[3]Range extension from Boreal Northwest Atlantic.

those in the present study within the 350-1,100 m depth interval. Respectively, the family Macrouridae accounted for 21% and 22.4% of the fishes captured in these depth intervals.

Haedrich and Krefft (1978) studied the fish fauna in the Denmark Strait and Irminger Sea. In the five fish assemblages that they reported, macrourids were abundant in the 2,026-2,058 m assemblage (22.4%) and very dominant in the 763-1,503 m (48.3%) and 493-975 m (55.4%) assemblages. Macrourids were conspicuously absent from their group three assemblage, although it was well within macrourid depth and temperature range (280-776 m, 1.4°7.4°C). An interesting aspect of Haedrich and Krefft's (1978) study was evident in their group two assemblage. *Coryphaenoides rupestris* was the highly dominant fish (48.3%) in this group, and the temperature range of this group (3.9°5.6°C) corresponded closely to the temperature range we found for *C. rupestris* in the present study (3.7°5.7°C).

Pearcy et al. (1982) summarized data on deep-sea benthic fishes collected over several years off Oregon (Day and Pearcy 1968; Pearcy and Ambler 1974). Iwamoto and Stein (1974) reported 11 species of macrourids from the northeast Pacific and Pearcy et al. (1982) recorded 8 of these off Oregon. A comparison of these data with ours shows that the greatest contrast in the two areas is on the upper and middle slope (500-1,000 m) where five common species are regularly encountered in the western Atlantic (*Coelorinchus c. carminatus, Nezumia bairdii, C. aequalis, Coryphaenoides rupestris,* and *Ventrifossa occidentalis*), but Pearcy et al. (1982) recorded no macrourid as common. This faunal difference may be due to the high density off Oregon of scorpaeniform and lycodine fishes, many of which may fill niches on the upper slope occupied by macrourids elsewhere. The macrourid fauna in depths >2,000 m have many similarities to our study. *Coryphaenoides armatus* becomes increasingly dominant below this depth and often is the only species captured deeper than 3,000 m in both areas (see also Musick and Sulak 1979). Among other macrourid species *Coryphaenoides leptolepis* is usually second or third in abundance at abyssal depths in both regions (Musick and Sulak 1979).

This distribution pattern is very different from that reported for the continental rise in the tropics off west Africa (Merrett and Marshall 1981) where *C. armatus* and other large rat tails were very rare. Marshall and Merrett (1981) speculated that the rarity of large predatory scavengers in the upwelling area they studied might be because of the competitively superior fishes of small size which were better adapted to use the constant abundant food supply there. This speculation is not supported by data from the southern Sargasso Sea and Bahamas (Musick and Sulak unpubl. data), a tropical region quite low in productivity, in which large rat tails, such as *C. armatus*, are also very rare. The virtual absence of *C. armatus* from tropical abyssal areas may be due instead to some restriction on the life history of the species. Musick and Sulak (1979) have suggested that this species (along with some other large species of predator/scavenger such as *C. rupestris* and *Antimora rostrata*) may migrate to boreal areas to spawn. The tropics may be too far removed from such spawning areas for individuals to successfully return.

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LITERATURE CITED

BEVERTON, R. J. H., AND S. J. HOLT.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food (G.B.) Ser. II 19, 533 p.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 557 p.

BULLIS, H. R., JR., AND P. T. STRUHSAKER.
1970. Fish fauna of the Western Caribbean upper slope. Q. J. Fla. Acad. Sci. 33(1):43-76.

CHRISTENSEN, J. M.
1964. Burning of otoliths, a technique for age determination of soles and other fish. J. Cons. Int. Explor. Mer 29:73-81.

DAY, D. S., AND W. G. PEARCY.
1968. Species associations of benthic fishes on the continental shelf and slope off Oregon. J. Fish. Res. Board Can. 25:2665-2675.

FARRON, G. P.
1924. Seventh report on the fishes of the Irish Atlantic Slope. The macrourid fishes (*Coryphaenoididae*). Proc. R. Ir. Acad., 36 Sect. B.

GATIEN, M. G.
1976. A study in the slope water region south of Halifax. J. Fish. Res. Board Can. 33:2213-2217.

GEISTDOEFER, P.
1975. Ecologie alimentaie des Macrouridae. Teleosteens Gadiformes. Ph.D. Thesis, Univ. Paris, Paris, France, 315 p.

GILBERT, C. H., AND C. L. HUBBS.
1920. The macrourid fishes of the Phillippine islands and the East Indies. U.S. Natl. Mus. Bull. 100, 1(pt. 7):369-582.

GOODE, G. B., AND T. H. BEAN.
1885. Descriptions of new fishes obtained by the United States Fish Commission mainly from deep water off the Atlantic and Gulf Coast. Proc. U.S. Natl. Mus. 8:589-605.

GORDON, J. D. M.
1979. Phenology of deep-sea anacanthine fishes. *In* P. J. Miller (editor), Fish phenology: anabolic adaptiveness in teleosts, p. 327-359. Symp. Zool. Soc. Lond., Acad. Press, N.Y.

GRIGOR'EV, G. V.
1972. Orazmnozhenii tuporylogo makrurusa severnoi Atlantiki (Reproduction of *Macrurus rupestris* (Gunner) of the northern Atlantic). Tr. Polyarn. Nauchno-Issled. Proektn. Inst. Morsk. Rybn. Khoz. Okeanogr. (PINRO) 289:107-115. (Engl. transl., Fish. Res. Board Can., Transl. Ser. 2529.)

GUNNERUS, J. E.
1765. Efterretning OM berglaxen, en rar norsk fishk, som kunde kaldes: *Coryphaenoides rupestris*. K. Nor. Vidensk. Selsk. Skr. Trondhjem 3(4):40-58.

GUNTHER, A.
1887. Report on the deep-sea fishes collected by H.M.S. *Challenger* during the years 1873-76. Report on the scientific results of the voyage of H.M.S. *Challenger*. Zoology 22:1-335.

HAEDRICH, R. L., AND N. R. HENDERSON.
1974. Pelagic food of *Coryphaenoides armatus*, a deep benthic rattail. Deep-Sea Res. 21:739-744.

HAEDRICH, R. L., AND G. KREFFT.
1978. Distribution of bottom fishes in the Denmark Strait and Irminger. Deep-Sea Res. 25:705-720.

HAEDRICH, R. L., AND P. T. POLLONI.
1976. A contribution to the life history of a small rattail fish, *Coryphaenoides carapinus*. Bull. South. Calif. Acad. Sci. 75:203-211.

HAEDRICH, R. L., G. T. ROWE, AND P. T. POLLONI.
1975. Zonation and faunal composition of epibenthic populations on the continental slope south of New England. J. Mar. Res. 33:191-212.

IWAMOTO, T.
1970. The R/V "Pillsbury" deep sea biological expedition to the Gulf of Guinea, 1964-65. Macrourid fishes of the Gulf of Guinea. Stud. Trop. Oceanogr. Miami 4:316-431.

IWAMOTO, T., AND D. L. STEIN.
1973. A systematic review of the rattail fishes (Macrouridae: Gadiformes) from Oregon and adjacent waters. Occas. Pap. Calif. Acad. Sci. No. 111, 79 p.

KOBLENTZ-MISHKE, O. J., V. V. VOLKOVINSKY, AND J. G. KABANOVA.
1970. Plankton primary production of the world ocean. *In* W. S. Wooster (editor), Scientific exploration of the South Pacific, p. 183-193. Natl. Acad. Sci., Wash., D.C.

KULIKOVA, E. B.
1957. Growth and age of deep water fishes. *In* B. N. Nikitin (editor), Marine biology, p. 284-290. Tr. Inst. Okeanol. Akad. Nauk. SSSR 20. [Engl. trans., Am. Inst. Biol. Sci. 1959.]

LEIM, A. H., AND W. B. SCOTT.
1966. Fishes of the Atlantic Coast of Canada. Fish. Res. Board Can., Bull. 155, 485 p.

MARSHALL, N. B.
1965. Systematic and biological studies of the Macrourid fishes (Anacanthini-Teleostii). Deep-Sea Res. 12:299-322.
1971. Explorations in the life of fishes. Harv. Univ. Press, Camb., 204 p.

MARSHALL, N. B., AND T. IWAMOTO.
1973. Family Macrouridae. *In* Fishes of the western North Atlantic. Mem. Sears Found. Mar. Res., No. 1, part 6, p. 496-662.

MACPHERSON, E.
1979. Ecological overlap between macrourids in the western Mediterranean Sea. Mar. Biol. (Berl.) 53:149-159.

MCEACHRAN, J. D., AND J. DAVIS.
1970. Age and growth of the striped sea-robin. Trans. Am. Fish. Soc. 99:343-352.

MCLELLAN, T.
1977. Feeding strategies of the macrourids. Deep-Sea Res. 24:1019-1036.

MERRETT, N. R.
1978. On the identity and pelagic occurrence of larval and juvenile stages of rattail fishes (family Macrouridae) from 60°N, 20°W and 53°N, 20°W. Deep-Sea Res. 25:147-160.

MERRETT, N. E., AND N. B. MARSHALL.
1981. Observations on the biology of deep-sea bottom-living fishes collected off northwest Africa (08°27°N). Prog. Oceanogr. 9:185-244.

MUSICK, J. A.
1969. The comparative biology of two American Atlantic hakes, *Urophycis chuss* and *U. tennuis* (Pisces: Gadidae). Ph.D. Thesis, Harvard Univ., Cambridge, 150 p.

MUSICK, J. A., AND K. J. SULAK.
1979. Characterization of the demersal fish community of a deep-sea radioactive dump site. Contract Report submitted to the U.S. Environmental Agency. Va. Inst. Mar. Sci., 61 p.

MUSICK, J. A., C. A. WENNER, AND G. R. SEDBERRY.
1975. Archibenthic and abyssobenthic fishes. *In* May 1974 baseline investigations of deep water dumpsite 106 NOAA evaluation. Rep. 75-1, 388 p.

NODZYNSKI, J., AND C. ZUKOWSKI.
1971. Biological and technological characteristics of grenadier family fishes (Macrouridae) of the Northwestern Atlantic. Studia I Materially Series D, No. 5, p. 1-45.

OKAMURO, O.
1970. Fauna Japonica. Macrourina (Pisces). Acad. Press, Tokyo, 179 p.

PEARCY, W. G.
1975. Pelagic capture of abyssobenthic macrourid fish. Deep-Sea Res. 23:1065-1066.

PEARCY, W. G., AND J. W. AMBLER.
1974. Food habits of deep-sea macrourid fishes off the Oregon Coast. Deep-Sea Res. 21:745-759.

PEARCY, W. G., D. STEIN, AND R. CARNEY.
1982. The deep-sea benthic fish fauna of the northeastern Pacific Ocean on Cascadia and Tufts Abyssal Plains and adjoining continental slopes. Biol. Oceanogr. 1:375-428.

PHLEGER, G. F.
1971. Biology of macrourid fishes. Am. Zool. 11:419-423.

POKDRAZHANSKAYA, S. G.
1967. Feeding of *Macrurus rupestris* in the Iceland area. Ann. Biol. 24:197-198.
1971. Feeding and migrations of the roundnose grenadier, *Macrourus rupestris*, in the Northwest Atlantic and Icelandic waters. Int. Comm. Northwest Atl. Fish., Redb. Part III, p. 115-123.

POLLONI, P., R. HAEDRICH, G. ROWE, AND C. H. CLIFFORD.
1979. The size-depth relationship in deep ocean animals. Int. Rev. Gesamten Hydrobiol. 64:39-46.

RANNOU, M.
1975. Donnees nouvelles sur l-activite reproductrice cyclique des poissions benthiques bathyaux et abbyssaux. Acad. Sci. Paris, T281, Ser. D, p. 1023-1025.
1976. Age et croissance d'un poisson bathyal: *Nezumia sclerorhynchus* (Macrouridae Gadiformes) de la mer

d'Alboran. Cah. Biol. Mar. 17:413-421.

RANNOU, M., AND C. THIRIOT-QUIEVREUAX.
1975. Structure des otolithes D'un Macrouridae (poisson Gadiforme) Bathyal. Étude au microscope Électronique a Balayage. Ann. Inst. Oceanogr., Paris 51:195-201.

SAVVATIMSKII, P. I.
1971. Studies of the age and growth of roundnose grenadier (*Macrourus rupestris*) in the North Atlantic 1967-1970. Int. Comm. Northwest Atl. Fish., Redb. Part III, p. 125-138.
1972. O vozraste tuporylogo makrurusa severo-zapadnoi Atlantiki i vozmozhnom vliyanii promysla no ego chislennost' (The age of the rock grenadier in the northwest Atlantic and a possible influence of fisheries on its population numbers). Tr. Polyarn. Nauchno-Issled. Proektn. Inst. Morsk. Rybn. Khoz. Okeanogr. (PINRO) 28:116-127. (Engl. transl., Fish. Res. Board Can., Transl. Ser. 2491.)

SMITH, K. L., JR.
1978. Metabolism of the abyssopelagic rattail *Coryphaenoides armatus* measured *in situ*. Nature (Lond.) 274:362-364.

SMITH, K. L., JR., G. A. WHITE, M. B. LAVER, R. R. MCCONNAUGHEY, AND J. P. MEADOR.
1979. Free vehicle capture of abyssopelagic animals. Deep-Sea Res. 26A:57-64.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry: The principles and practice of statistics in biological research. W. H. Freeman and Co, San Franc., 776 p.

STANEK, E.
1971. Badania zasobow rybnych wod Labradora i Nowej Fundlandii (Studies on the fish stocks in the waters off Labrador and Newfoundland). Pr. Morsk. Inst. Rybackiego, p. 121-146. (Engl. trans., Fish. Res. Board Can., Transl. Ser. 2754.)

WEBSTER, F.
1969. Vertical profiles of horizontal ocean currents. Deep-Sea Res. 16:85-98.

WENNER, C. A., AND J. A. MUSICK.
1979. Biology of the morid fish *Antimora rostrata* in the western North Atlantic. J. Fish. Res. Board Can. 34:2362-2368.

WORTHINGTON, L. V.
1964. Anomalous conditions in the slope water area in 1959. J. Fish Res. Board Can. 21:327-333.

ZAKHAROV, G. P., AND I. D. MOKANU.
1970. Distribution and biological characteristics of *Macrourus rupestris* of the Davis Strait in August-September 1969. Reports of Pinro Marine Expeditionary Investigations, 3rd cruise of R/V *Perseus III*.

DIFFERENTIATION OF *PRIONOTUS CAROLINUS* AND *PRIONOTUS EVOLANS* EGGS IN HEREFORD INLET ESTUARY, SOUTHERN NEW JERSEY, USING IMMUNODIFFUSION

WALTER J. KEIRANS,[1] SIDNEY S. HERMAN,[2] AND R. G. MALSBERGER[2]

ABSTRACT

Immunochemical techniques were used to classify the planktonic eggs of *Prionotus carolinus* (northern searobin) and *Prionotus evolans* (striped searobin) collected from a southern New Jersey estuary. Results of immunochemical identifications were compared with identifications based upon the commonly used morphological character of egg oil globule distribution. An average identification error of 22.3% was found when results using this conventional morphological characteristic were compared with immunodiffusion results. Improved accuracy of searobin egg identification can be achieved in future ichthyoplankton studies by using immunochemical techniques. A similar application of immunochemical identification techniques should also better resolve classification uncertainties among other morphologically similar co-temporal and co-spatial planktonic fish eggs.

The accuracy of ichthyoplankton analysis is often limited by the lack of reliable, distinguishing, morphological characteristics that are useful for identifying fish eggs and larvae. Conventional characteristics used to identify fish eggs include egg and oil globule diameters; number, distribution, and pigmentation of oil globules; and pigmentation patterns on developing embryos. However, overlapping diameters of eggs and a similar if not identical number of oil globules with comparable pigmentation and size among closely related species impose a relatively high degree of uncertainty concerning the identity of planktonic fish eggs from many areas. Increased accuracy has been more recently achieved through the analysis of fish eggs using biochemical, immunological, and ontogenetic methods. Morgan (1975) examined electrophoretic patterns of white perch and striped bass egg extracts and found differentiation was possible on this basis. Orlowski et al. (1972) differentiated cunner, *Tautogolabrus adsperus*, from tautog, *Tautoga onitis*, eggs using monospecific antisera in microimmunodiffusion analyses. The technique was especially useful with early stage eggs which were morphologically identical. Ontogenetic methods allow careful study of laboratory-reared eggs and larvae of known parentage to document species-specific developmental histories. These studies may provide new distinguishing morphological features for future egg identifications. However, additional means are required where well-documented features shared with other species do not provide adequate differentiation of field-collected eggs.

This paper is a report on the results obtained from a microimmunodiffusion analysis which successfully differentiated the planktonic eggs of the northern searobin, *Prionotus carolinus*, from those of the striped searobin, *Prionotus evolans*, which were collected from the Hereford Inlet estuary, southern New Jersey, between May 1973 and September 1974 (Keirans 1977). Identifications based separately upon immunochemical and morphological evidence were also compared to evaluate the reliability of differentiations based entirely upon conventional morphology. *Prionotus* spp. were selected in our study first because the searobins represent a large breeding population which appears co-temporally and co-spatially near shore to provide an abundant source of gravid adults. Eggs of known parentage became readily available for preparation of experimental reagents and specimens. Secondly, this study would expand the application of microimmunodiffusion analysis to species differentiation as an extension of the study of Orlowski et al. (1972), which documented differentiation of eggs from two genera. Finally, the identification of *Prionotus* spp. ova has never been properly resolved.

Prionotus carolinus ova were described by Kuntz and Radcliffe (1918) as highly transparent but slightly yellowish spherical eggs ranging from 1.0 to 1.15 mm in diameter. The yolk sphere contained a

[1]Department of Biology, Lehigh University, Bethlehem, PA; present address: E. I. du Pont de Nemours Co., Inc, Glasgow Research Laboratory, Wilmington, DE 19898.
[2]Department of Biology, Lehigh University, Bethlehem, PA 18015.

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variable number of 10 to 25 unequal-sized oil globules scattered over the yolk surface which showed some tendency toward aggregation with progressing development. The diameter range was extended from 0.94 mm to 1.20 mm by Bigelow and Schroeder (1953) and Wheatland (1956), respectively. The upper diameter limit extension was verified by Herman (1963). *Prionotus evolans* ova have never been positively identified. Perlmutter (1939) made a tentative identification, later accepted by Marshall (1946), from ripe ova stripped from gravid females collected in Long Island Sound and described as having similar appearance and diameter as northern searobin eggs, but with oil globules clustered at one pole rather than dispersed across the yolk sphere surface. This singular observed morphological difference of oil globule distribution pattern has been used as the primary distinguishing characteristic between ova of *Prionotus carolinus* and *Prionotus evolans*.

MATERIALS AND METHODS

Conventional Identifications

Field-collected, buffered Formalin[3]-preserved plankton samples were physically sorted for all ichthyoplankton using forceps under a dissecting microscope, and the criterion of oil globule distribution differences established by Perlmutter (1939) was used to tentatively separate *P. carolinus* from *P. evolans* eggs. The annual cycle and species composition aspects of the field-collected samples using conventional means for egg and larval identifications have been submitted elsewhere for publication.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Immunochemical Identifications

Antigens and Immunizations

Antigen preparations from both species of searobin eggs were generated using the techniques developed by Orlowski et al. (1972) with ovarian tissue from ripe adults and immature individuals. The four antigen preparations presented in detail in Table 1 were each used to elicit immune responses in at least two New Zealand white rabbits to improve the probability of obtaining useful antisera. Preimmune serum samples were obtained from each animal to establish that no reactivity with antigen existed prior to immunization.

The soluble protein antigens of *Prionotus evolans* (PeSP) and *Prionotus carolinus* (PcSP) were injected intravenously in 4.7 and 4.8 mg protein doses (standard biuret analysis), respectively, to begin the immunization program. Maintenance injections of 2 mg protein followed on a weekly basis. Blood samples were obtained by cardiac puncture 3 wk following the first injection and the presence of precipitating antibody was demonstrated by the standard precipitin ring test (Abramoff and LaVia 1970). Additional monthly cardiac puncture samples were monitored by quantitative double diffusion (Feinberg 1957) until after about 12 wk; a titer of 32 was reached in all animals receiving soluble antigens when sera were tested with 40 μg homologous antigen.

Particulate protein antigens from macerated ovarian tissue of northern (PcPP) and striped (PePP) searobins were prepared in a 1:1 emulsion with Freund's complete adjuvant (Cappell Laboratories). PcPP (8 mg) and PePP (10 mg) protein preparations were injected subcutaneously along several bilateral dorsal sites on New Zealand white rabbits. Rabbits injected with Freund's complete adjuvant developed

TABLE 1.—Antigen characterization and nomenclature.

Species	Antigen source and designation	Range protein concentration (mg/mL)	Method of determination	Immunization route and dose		Titer	
				Initiation	Maintenance	Double-diffusion	Complement fixation
Prionotus carolinus Northern searobin	Mature ova (PcSP)	8-15	Biuret	Intravenous (4.7 mg)	Intravenous (2 mg)	32	
	Immature follicular material (PcPP)	15-40	Microkjeldahl	Subcutaneous (8 mg)	Intravenous (2 mg)		1,280
Prionotus evolans Striped searobin	Mature ova (PeSP)	8-15	Biuret	Intravenous (4.8 mg)	Intravenous (2 mg)	32	
	Immature follicular material (PePP)	15-40	Microkjeldahl	Subcutaneous (10 mg)	Intravenous (2 mg)		1,280

Arthus reactions following a single dose. Subsequent injections were accomplished intravenously using Millipore (0.45 μm) filtrates of PcPP and PePP. Titers were monitored utilizing the standard complement fixation assay because of the particulate consistency of the macerated antigen preparation (Kabat and Mayer 1961). Maximum titers of 1,280 were obtained after about 10 wk with immunizations using PcPP or PePP.

Antiserum Specificity

Antisera elicited in response to both soluble and particulate antigens were multicompetent and exhibited cross-reactions with heterologous antigens. The presence of common antigens between the northern searobin and striped searobin ovarian material preparations required the specific adsorption of antisera with these shared antigens to render a given antiserum monospecific (Eisen 1974). Although antisera elicited in response to particulate protein antigens exhibited precipitation reactions in agar with both soluble antigens and extracts of particulate antigens from the two species under consideration, they were not competent in reactions with homologous fish eggs. Therefore, since the selected method for analysis of planktonic eggs was immunodiffusion, only antisera elicited in response to soluble antigens were used in all analyses of unknowns. Specific adsorption of common antigens shared by northern and striped searobins was accomplished by adding PcSP to antisera elicited in response to PeSP and vice versa. Adsorption lots of 1.5 mL anti-PeSP antisera combined with 70 μL PcSP (0.65 mg protein) were incubated at 4°C for 48 h prior to use. This adsorption eliminated all reactivity of anti-PeSP antisera with both PcSP and known ova of *P. carolinus*, without significantly reducing activity with ova of *P. evolans*. This specifically adsorbed anti-PeSP, which reacted solely with known homologous ova of *P. evolans* under controlled conditions, was used as the basis for differentiation of northern and striped searobin eggs. Species-specific anti-PeSP antisera capable of 100% accuracy in differentiating known ova of both searobins was the reagent selected for use in all immunodiffusion analyses.

Microimmunodiffusion Analysis

Unknown planktonic fish eggs were analyzed with monospecific anti-PeSP antiserum in a micromodification of the immunodiffusion technique (Ridgeway et al. 1962). Microscope slides (2.5 × 8 cm) were washed, rinsed first in distilled water and then methanol, and wiped dry. Two milliliters of 1% Noble Agar (Difco) in FA-Bacto buffer (Difco), pH 7.2, were applied across each slide on a leveling table and allowed to harden. Slides were then placed over a template and wells cut using a Brewer needle with beveled inner surface (Ridgeway et al. 1962).

Agar plugs were removed from wells by aspiration. Reagents were applied with either 1 mL syringes (Burron) or sterile capillary pipettes, and 0.005 to 0.01 mL was required to fill each well. A typical testing array appears in Figure 1, where corner wells contain unadsorbed antiserum, the central well contains adsorbed or monospecific antiserum, and remaining wells contain individual fish eggs which have been broken using jeweler's forceps. FA-Bacto buffer was applied to each well following egg disruption, and slides were allowed to incubate in moist chambers for 18 h at 20°C. Slides were then washed for 24 h in FA-Bacto buffer, and stained according to the method of Crowle (1958). Results were always recorded at a fixed time interval following slide preparation to insure comparability from one determination to another.

RESULTS AND DISCUSSION

A total of 732 searobin ova were recovered from plankton samples collected in the 1973-74 period. The combined morphological characteristics of egg diameter, number, color, and distribution of oil globules, and embryo pigmentation when present, allowed the separation of searobin eggs from those of other species with reasonably high confidence. Preliminary classifications of *Prionotus* ova into either *evolans* or *carolinus* species was based upon differential oil globule distribution patterns reported by Perlmutter (1939). Striped searobin, *P. evolans*, eggs were placed into one grouping based upon a polar or clustered oil globule distribution, and northern searobin, *P. carolinus*, eggs placed into a second group having oil globules generally dispersed across the yolk sphere.

Each tentatively classified egg was then analyzed in the microimmunodiffusion method illustrated in Figure 1, to establish the immunochemical reactivity of soluble egg antigens with adsorbed and unadsorbed anti-PeSP antisera. When soluble *P. evolans* egg antigens were sufficiently concentrated, a classical line of identity was observed with fusion of precipitin bands between adsorbed and unadsorbed anti-PeSP wells. Identification of *P. carolinus* eggs was based upon reactivity with unadsorbed anti-PeSP antiserum and no reactivity with adsorbed anti-PeSP. Previously established reactivity of unadsorbed anti-

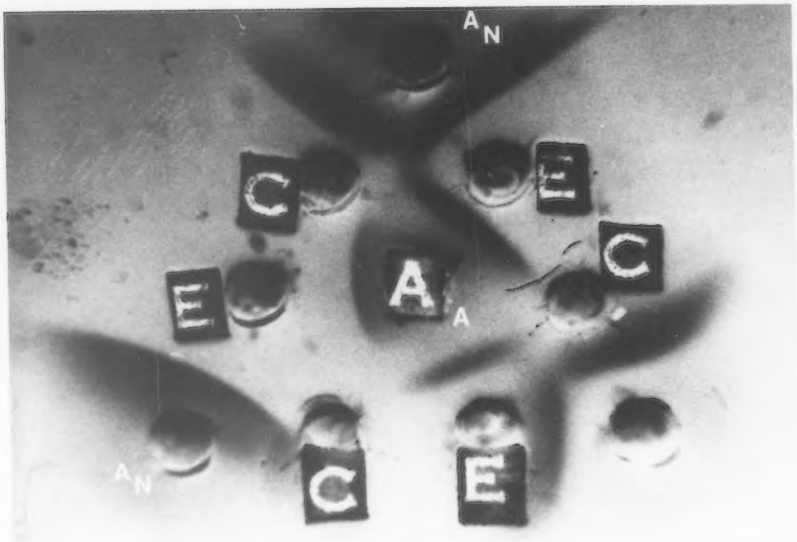

FIGURE 1.—Testing array (10×). C: *Prionotus carolinus* ovum (1.00 mm); E: *Prionotus evolans* ovum (1.00 mm); A_A: Anti-PeSP antiserum (adsorbed: 0.20 mL antiserum: 0.11 mg PcSP protein); A_N: Anti-PeSP antiserum (unadsorbed). Specific adsorption of cross-reactive antibodies has occurred with PcSP, rendering anti-PeSP antiserum (A_A) incompetent to react with antigens of *Prionotus carolinus* ova (C), indicated by the lack of precipitin bands about the central well adjacent to (C) egg wells. Corner wells contain multicompetent, unadsorbed anti-PeSP antisera.

PeSP with known *P. carolinus* eggs was considered sufficiently definitive for its use in differentiating *P. carolinus* from *P. evolans* ova.

The immunochemical classifications derived from this analysis indicated that an average 22.3% misclassification error had been made when eggs were differentiated solely on the basis of oil globule distributions. An approximately equal number of both northern and striped searobin eggs had been mistakenly identified, based upon oil globule distribution patterns. The final classification based upon immunochemical data was 406 ova of *P. carolinus* and 326 ova of *P. evolans*.

It was confirmed that egg diameters could not serve as a reliable characteristic for species classifications by retrospectively analyzing diameters of immunochemically classified eggs according to the period of field collection. The data presented in Table 2 illustrate that no statistical difference exists in the diameter ranges of *P. carolinus* and *P. evolans* eggs for the collection period of this study. However, the trend of declining egg diameters over the spawning season previously documented by other workers is

TABLE 2.—Immunochemical classification of *Prionotus* spp. eggs collected in plankton samples.

Date	Average diameter (mm)	Range (mm)	*n*
Prionotus carolinus			
1973			
May	1.16	1.02-1.24	4
June	1.06	1.00-1.21	10
July	1.08	1.05-1.10	3
August	1.02	0.92-1.18	312
September	0.99	0.90-1.05	32
1974			
July	0.98	0.95-1.02	13
August	0.96	0.92-1.02	3
September	0.99	0.92-1.02	29
Prionotus evolans			
1973			
May	1.12	1.00-1.25	10
June	1.06	1.00-1.12	35
July	1.08	1.00-1.15	2
August	1.03	0.95-1.12	225
September	0.98	0.90-1.08	26
1974			
July	0.97	0.95-1.00	6
August	1.02	1.02	1
September	0.99	0.92-1.02	21

confirmed. The data also show that in 1973 and 1974, the ratios of eggs collected in plankton samples and identified based upon morphology and immunochemical reactions for nothern and striped searobins were 1.1:1 and 1.6:1, respectively. These ratios are similar in magnitude to the ratio of northern and striped searobin adults observed by Marshall (1946). Finally, the data indicate that egg diameter and oil globule distribution cannot serve to reliably distinguish northern from striped searobin eggs. An immunochemical distinction can be made that suggests morphology alone is inadequate to provide a positive identification of *P. evolans* eggs.

The course of future research in immunochemical taxonomy of fish eggs should emphasize an increase in sensitivity, as well as automation of the analysis. At present, the utility of the immunodiffusion method is limited by its labor-intensive nature. Initial stages of the analysis require manual sorting of ova from plankton samples that is tedious, time-consuming, and subject to error. Bowen et al. (1972) initiated studies in which a moderate degree of success was achieved in sorting fish ova from pelagic plankton samples on sucrose density gradients. However, estuarine plankton samples that contained a wide range of particulate materials characterized by different sizes, densities, and shapes, and that also included high levels of detrital materials, disturbed the gradients sufficiently to destroy separation potential. Despite the recognized limitations, there is currently no practical alternative to manual sorting of plankton samples.

Immunodiffusion analysis requires that individual fish eggs be subjected to several manual manipulations, with the final determination in solid media requiring the careful applications of reagents. Screening large numbers of planktonic ova with several different antisera becomes impractical on a large scale. A more rapid and potentially more specific approach to immunochemical ichthyoplankton identifications might employ monoclonal antibodies coupled to fluorescent indicator molecules. The antibody products of fused mouse lymphocytes and myeloma cells may be screened and selected for exquisite specificity to single antigenic determinants or epitopes using egg antigens of known origin, preferably those associated with the chorion surface, to procure a reagent that would specifically label ova without requiring that each egg be mechanically ruptured. Identifications might be based upon the differential fluorescence characteristic of a particular fluorescent label associated with a selected antibody and labelled eggs might be isolated using a fluorescence-activated cell sorter.

The utility of immunochemical identifications with demonstrably superior accuracy to conventional methods has been established with both intergeneric and interspecific differentiations. Several systems remain which might benefit from immunochemical differentiations, such as the complete elucidation of several sciaenid and clupeid species which occur in complex estuarine systems, such as the Chesapeake Bay and Potomac River estuary. Relationships between scombrids, bothids, and pleuronectids with more southerly distributions would serve to delineate adult ratios, population distributions, and spawning seasons. Finally, the capability of the immune system to differentiate among epitopes with relatively small structural difference (Karush 1962) might eventually be applied to the detection of racial differences or subpopulation distinctions among fish ova of the same species.

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LITERATURE CITED

ABRAMOFF, P., AND M. LAVIA.
1970. Biology of the immune reponse. McGraw-Hill, Inc, N.Y., 492 p.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53:1-577.

BOWEN, R. A., J. M. ST. ONGE, J. S. COLTON, JR., AND C. A. PRICE.
1972. Density-gradient centrifugation as an aid to sorting planktonic organisms. I. Gradient materials. Mar. Biol. (Berl.) 14:242-247.

CROWLE, A. J.
1958. A simplified micro double-diffusion agar precipitin technique. J. Lab. Clin. Med. 52:784-787.

EISEN, H. N.
1974. Immunology: An introduction to molecular and cellular principles of the immune responses. Med. Dep., Harper & Row, Inc., Hagerstown, MD, 624 p.

FEINBERG, J. G.
1957. Identification, discrimination, and quantification in Ouchterlony gel plates. Int. Arch. Allergy 11(3-4):129-152.

HERMAN, S. S.
1963. Planktonic fish eggs and larvae of Narragansett Bay. Limnol. Oceanogr. 8:103-109.

KABAT, E. A., AND M. M. MAYER.
1961. Complement and complement fixation. Experimental immunochemistry. 2d ed. Chase Thomas Publ., Springfield, IL, 905 p.

KARUSH, F.
1962. Immunologic specificity and molecular structure. Adv. Immunol. 2:1-40.

KEIRANS, W. J., JR.
1977. An immunochemically assisted ichthyoplankton survey with elaboration on species specific antigens of fish egg

vitellins; southern New Jersey Barrier Island - Lagoon Complex. Ph.D. Thesis, Lehigh Univ., Bethlehem, PA 169 p.

KUNTZ, A., AND L. RADCLIFFE.
1918. Notes on the embryology and larval development of twelve teleostean fishes. Bull. U.S. Bur. Fish. 35:89-134.

MARSHALL, N.
1946. Observations on the comparative ecology and life history of two sea robins, *Prionotus carolinus*, and *Prionotus evolans strigatus*. Copeia 1946:118-144.

MORGAN, R. P., II.
1975. Distinguishing larval white perch and striped bass by electrophoresis. Chesapeake Sci. 16:68-70.

ORLOWSKI, S. J., S. S. HERMAN, R. G. MALSBERGER, AND H. N. PRITCHARD.
1972. Distinguishing cunner and tautog eggs by immunodiffusion. J. Fish. Res. Board Can. 29:111-112.

PERLMUTTER, A.
1939. A biological survey of the salt waters of Long Island, 1938. Section I. An ecological survey of young fish and eggs identified from tow-net collection. Suppl. 28th Annu. Rep. N.Y. Conserv. Dep. Part II:11-71.

RIDGEWAY, G. J., G. W. KLONTZ, AND C. MATSUMOTO.
1962. Intraspecific differences in serum antigens of red salmon demonstrated by immunochemical methods. Int. North Pac. Fish. Comm. 8:1-13.

WHEATLAND, S. B.
1956. Oceanography of Long Island Sound. 1952-1954. VII. Pelagic fish eggs and larvae. Bull. Bingham Oceanog. Coll., Yale Univ. 15:234-314.

EFFECTS OF EXPOSURE AND CONFINEMENT ON SPINY LOBSTERS, *PANULIRUS ARGUS*, USED AS ATTRACTANTS IN THE FLORIDA TRAP FISHERY

JOHN H. HUNT,[1] WILLIAM G. LYONS,[2] AND FRANK S. KENNEDY, JR.[2]

ABSTRACT

Traps in the south Florida spiny lobster fishery are baited with live sublegal-sized lobsters (shorts), many of which are exposed for considerable periods aboard vessels before being placed in traps and returned to the sea. Average mortality rate of lobsters exposed ½, 1, 2, and 4 hours in controlled field tests was 26.3% after 4 weeks of confinement. About 42% of observed mortality occurred within 1 week after exposure, indicating exposure to be a primary cause of death. Neither air temperature during exposure nor periodic dampening with seawater had significant effects on mortality rate. Mortality among confined lobsters increased markedly in the Atlantic oceanside but not in Florida Bay during the fourth week of confinement following exposure, probably because more natural food organisms entering traps from nearby seagrass beds delayed starvation at the latter site. Mortality caused by baiting traps with shorts may produce economic losses in dockside landings estimated to range from $1.5 to $9.0 million annually.

The fishery for spiny lobster, *Panulirus argus*, in south Florida utilizes a method of baiting traps that is apparently unique among fisheries worldwide. Sublegal [<76 mm carapace length (CL)] lobsters, locally called "shorts", are confined in traps as living attractants for legal-sized lobsters. Shorts have been demonstrated to be effective attractants of other lobsters (Yang and Obert 1978; Lyons and Kennedy 1981; Kennedy 1982). Some use of shorts as bait in the Florida fishery occurred as early as the 1950's (Cope 1959), but use increased appreciably after 1965 when the minimum legal size was reduced from 1 lb (about 79-80 mm CL) to 3 in (76 mm) CL, and the fishery expanded from Atlantic oceanside reefs and flats into Florida Bay where availability of shorts is considerably greater (Lyons et al. 1981). The practice was widespread but illegal during early years of its use (Wolfferts 1974) and only received legal sanction in 1977. Today, bonded fishermen are allowed to possess as many as 200 shorts aboard a vessel for use as bait. Shorts are customarily kept in wooden boxes on deck until replaced in traps, and exposure times vary from several minutes to 1 h or more. As many as 1 million shorts may be confined in traps as bait during peak portions of the harvest season (Lyons and Kennedy 1981).

During 1979, the Florida Department of Natural Resources initiated a study in which baiting practices in the fishery were mimicked under controlled conditions to determine whether starvation occurred among lobsters confined in traps for long periods. So much mortality occurred among tested lobsters during the first 2 wk of confinement that the study was redirected toward causes of that mortality. Exposure was strongly implicated by preliminary results (Lyons and Kennedy 1981). Spokesmen for the fishing industry suggested that observed mortality was caused by other factors related to experimental design, prompting expansion of the program to test those factors.

This report presents results and conclusions from that expanded program. The relationship between exposure and mortality is examined, including influences of season and location. Mortality rates of lobsters held dry or periodically dampened prior to placement in traps are also compared. Results from this study are used in a model which estimates the relative importance of baiting mortality to economics of the fishery.

METHODS

Mortality rates of spiny lobsters used to bait traps were measured in Florida Bay 3 km north of Vaca Key and in the Atlantic Ocean 6 km south of Vaca Key. The Florida Bay site was located in shallow water (~3 m) with a muddy sand substrate overlain by seagrass beds. The ocean site was located in

[1]Florida Department of Natural Resources, Bureau of Marine Research, Marathon, FL 33050.
[2]Florida Department of Natural Resources, Bureau of Marine Research, St. Petersburg, FL 33701.

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deeper water (~8 m) just inside the reef tract; the bottom consisted of a mosaic of scattered seagrasses, small patch reefs, and open areas of coarse sand. Salinities at both sites ranged from 34‰ to 36‰ and water temperature ranged seasonally from 17° to 29°C.

The effect of exposure was examined at both sites. Lobsters were held in shaded boxes for ½, 1, 2, and 4 h and then placed in traps. Entrances were sealed, and no lobsters were added after treatments were established. Each treatment utilized 5 standard wooden slat lobster traps; each trap contained 3 lobsters (total 15 lobsters/treatment) for each exposure period. Control treatments (minimum exposure) also consisted of 5 traps each containing 3 lobsters, but these lobsters remained in traps in which they were originally captured and were exposed only for the time required to clean, seal, and return a trap to the water. Intent was to place sublegal lobsters in all traps, but use of some larger lobsters was necessary to conduct experiments. Traps in oceanside experiments were reinforced with wire mesh sides to reduce damage by loggerhead turtles, *Caretta caretta*; traps in Florida Bay were not reinforced with wire sides.

In Florida Bay, all lobsters exposed ≥1 h were dampened every ½ h by pouring a bucket of seawater into the porous holding box, whereas equal numbers of lobsters exposed ≥1 h in oceanside tests were always treated with and without seawater dampening every ½ h to test the effect of dampening. Control and ½-h treatments were the same in dampened (wet) and undampened (dry) tests because their total exposure periods were less than or equal to the period between dampenings.

After initiation, all experiments were sampled at 1-wk intervals for 4 wk by pulling each trap and counting remaining live lobsters. The mortality estimate is a combination of missing lobsters and those observed to be dead. Several lines of evidence indicate that missing lobsters died and did not escape. Only lobsters too large to fit between trap slats were used in experiments, and trap entrances were boarded shut to seal the ordinary avenue of departure. Additionally, observations made during frequent dives at traps where lobsters died during other experiments indicated that carcasses could be broken up sufficiently by scavengers within 24 h after death to wash through slats when traps were pulled.

All original data, taken as number of living lobsters remaining in a trap each week, were converted to weekly mortality rates calculated as the number of lobsters that died during that week divided by the initial density during that week. This method provided the only independent, noncumulative estimate of mortality. All other methods biased the data by either increasing the weight given to deaths later in the experiment or altering mortality estimates because of trap losses. Although this method provided unbiased estimates of mortality, data still were not normally distributed, so all testing of treatment means used nonparametric Wilcoxon Two Sample Tests (Sokal and Rohlf 1969) to determine where the differences of significance occurred. Standard notations are used to designate signi-

TABLE 1.—Average weekly spiny lobster mortality (%) for each location, exposure period, and wet or dry treatment. N = number of traps; $\bar{x}$ = mean; SE = standard error; W = wet; D = dry.

Treatment		Initial	Week after initial exposure												Cumulative mortality
			Week 1			Week 2			Week 3			Week 4			
		N	N	$\bar{x}$	SE	N	$\bar{x}$	SE	N	$\bar{x}$	SE	N	$\bar{x}$	SE	%
Florida Bay															
Control		15	15	0.0	0.0	15	0.0	0.0	15	2.2	2.2	15	0.0	0.0	2.2
½ h		20	20	8.3	5.3	19	3.5	3.5	18	0.0	0.0	17	0.0	0.0	11.8
1 h	W	20	17	7.8	3.5	17	3.9	3.9	16	6.2	3.4	16	6.2	6.2	24.1
2 h	W	20	18	14.8	5.5	18	1.8	1.8	18	1.8	1.8	18	3.7	2.5	22.1
4 h	W	20	20	15.0	5.6	19	5.3	2.9	19	5.3	2.9	18	0.0	0.0	25.6
Atlantic Reef															
Control		29	28	4.8	2.8	23	1.4	1.4	23	0.0	0.0	27	7.4	3.2	13.6
½ h		29	29	8.0	3.6	24	1.4	1.4	23	4.3	4.3	27	12.3	4.8	26.0
1 h	W	29	29	16.1	4.8	24	9.7	3.7	19	7.0	4.1	24	12.5	5.2	45.3
	D	29	29	11.5	3.8	24	9.7	5.1	22	4.5	2.5	27	11.1	5.3	36.8
2 h	W	29	29	13.8	5.1	17	3.9	2.7	15	4.4	3.0	20	5.0	2.7	27.1
	D	29	29	16.1	5.4	23	5.8	2.7	22	4.5	2.5	24	5.6	3.3	32.0
4 h	W	29	29	12.6	3.8	23	4.3	3.2	19	8.8	6.2	22	6.1	2.8	31.8
	D	29	29	11.5	4.1	21	7.9	4.5	18	1.8	1.8	23	1.4	1.4	22.6

ficance at probability levels of 0.05, 0.01, and 0.001.

Weighted cumulative average mortality values were obtained by multiplying the relative effort (%) in each treatment (e.g., site, exposure period ≥½ h) by the cumulative mortality for that treatment and then summing those values.

RESULTS

The mortality experiment was conducted four times between January and September 1980 in Florida Bay and six times between May 1981 and June 1982 near Atlantic reefs. Wet vs. dry tests were conducted with each oceanside replicate. The unweighted average cumulative mortality calculated from Table 1 for all lobsters exposed ½, 1, 2, and 4 h, both sites combined, was 26.3% at the end of 4 wk. Average weighted cumulative mortality in Florida Bay was 20.8%, and that near Atlantic reefs was 31.9%. When weighted for relative effort at each site, the overall mortality rate increased to 28.5%.

No tests were established at oceanside stations during December, January, or February, so effects of air and water temperatures on mortality during exposure were tested only in Florida Bay. Of four tests conducted there, two were established during cool months (January, February; air 15.2°-21.0°C, water 17.0°-17.5°C during initiation), and two were established during warm months (May, September; air 27.6°-33.5°C, water 29.3°-29.5°C). Mean weekly mortality rates of lobsters during these tests (winter $\bar{x}$ = 4.4%; summer $\bar{x}$ = 4.6%) were not significantly different.

Average mortality rates obtained in wet vs. dry treatments (Table 1, Fig. 1) were not significantly different for any exposure or subsequent confinement period. Furthermore, neither wet nor dry treatments consistently caused greater mortality.

Because all Florida Bay lobsters were dampened when exposed ≥1 h, comparisons of bay vs. ocean mortality rates were made using wet treatments only. All five treatments (Control, ½, 1, 2, and 4 h) were combined and overall mean weekly mortality rates were compared. The average weekly mortality rate of lobsters in bay tests ($\bar{x}$ = 4.5%) differed significantly ($Z = 2.51$, $P < 0.05$) from that of lobsters tested in the ocean ($\bar{x}$ = 7.6%).

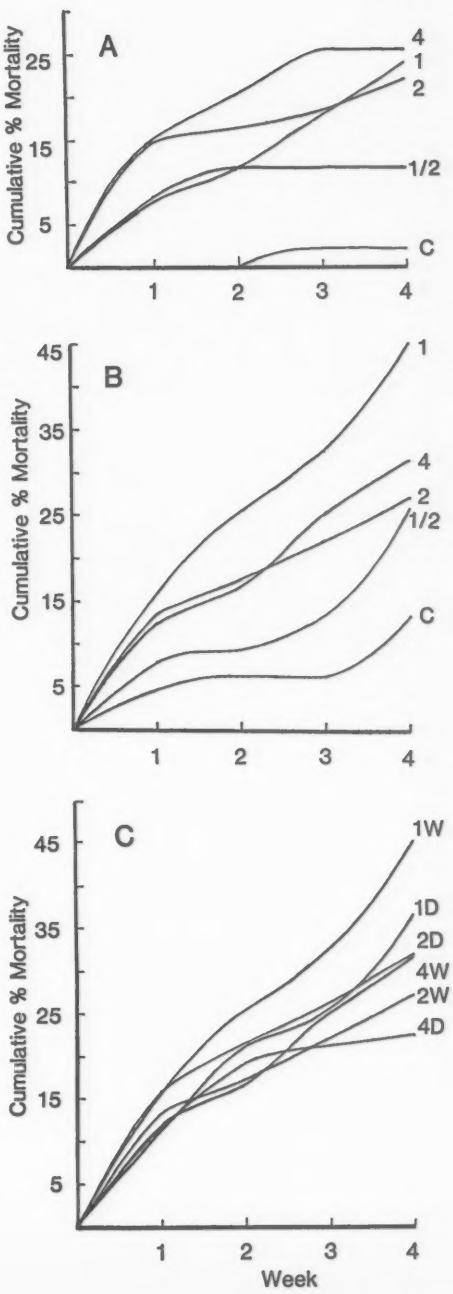

FIGURE 1.—Cumulative mortality rates (%) for exposure tests: A. Florida Bay, wet only; B. Atlantic reefs, wet only; C. Wet (W) vs. dry (D), Atlantic reefs only. C = controls; exposure periods = ½, 1, 2, and 4 h.

Comparisons of each exposure period within a treatment with every other exposure period within that treatment are shown in Table 2. In the bay, mortality rates experienced by controls were significantly different than those of lobsters exposed 1, 2, or 4 h. Additionally, lobsters exposed ½ h suffered a significantly lower mortality rate than did those exposed 4 h. However, some of these differences were not significant among lobsters exposed at the Atlantic reef site. Among dampened lobsters tested there, only the mortality rate of those exposed 1 h differed significantly from that of controls and from that of lobsters exposed ½ h. Among undampened lobsters tested at the ocean site, mean mortality rates of controls differed significantly only from those exposed 1 or 2 h. Differences between controls and 1 h exposures were significant in every treatment, but mean mortality rates never differed significantly among lobsters exposed 1, 2, or 4 h.

The mean mortality rate of all tested lobsters during the first week following exposure was 11.2%, which represents about 42% of all mortality; 54% of all mortality in Florida Bay and 38% of all which took place near Atlantic reefs occurred during the first week (Table 1, Fig. 1). High mean weekly mortality rates which occurred during week 1 decreased to much lower levels during week 2 (4.7%) and week 3 (3.9%) in both bay and ocean (Fig. 2). Comparisons of mean mortality rates incurred during week 1 with those of weeks 2 and 3 revealed significant differences in every instance (Table 3). During week 4, the overall rate increased to 6.1% (Fig. 2), but this combined value masked highly divergent changes in rates of mortality at bay and ocean sites.

TABLE 2.—Results of Wilcoxon Two Sample Tests (*Z* values) from comparisons of mean weekly mortality rates from different exposure periods for various treatments at Florida Bay (Bay) and Atlantic Reef (Ocean) locations. C = controls; exposure = hours.

Tests	Exposure	C	½	1	2	4
Bay wet	C	—				
	½	1.14	—			
	1	2.48*	1.62	—		
	2	2.52*	1.68	0.02	—	
	4	2.93**	2.17*	0.51	0.49	—
Ocean wet	C	—				
	½	1.10	—			
	1	3.07**	2.02*	—		
	2	1.87	0.81	1.17	—	
	4	1.93	0.85	1.16	0.03	—
Ocean dry	C	—				
	½	1.10	—			
	1	2.20*	1.12	—		
	2	2.12*	1.03	0.10	—	
	4	1.17	0.08	1.01	0.92	—

* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$.

Bayside mortality rates actually decreased slightly, whereas oceanside rates increased dramatically. Statistical comparisons between mean mortality rates during weeks 1 and 4 demonstrate significant differences in the bay but not in the ocean (Table 3). Graphic depictions of cumulative weekly mortality rates (Fig. 1) reveal a decrease in slope after week 1 at both bay and ocean sites. These decreases indicate reduced rates of mortality which persist through the end of the experiment in the bay and through week 3 in the ocean. However, the slope increases sharply during week 4 in most oceanside tests, indicating an additional period of high mortality there.

DISCUSSION

Exposure unquestionably causes mortality among *Panulirus argus* used to bait traps. Increasing ex-

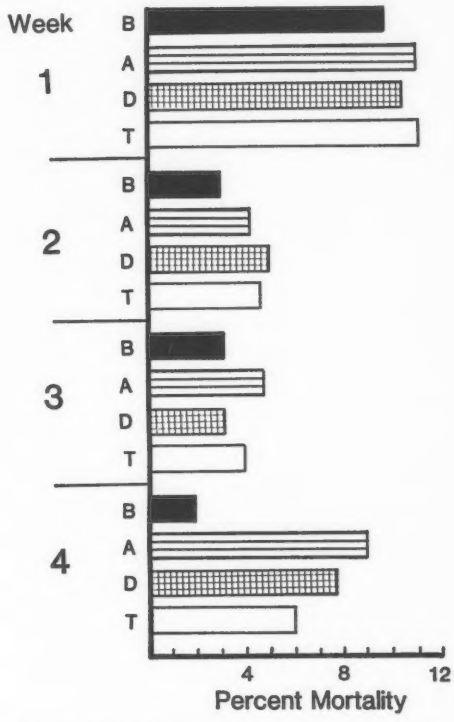

FIGURE 2.—Average weekly mortality rates (%) per treatment type during weeks 1-4, all exposures combined. A = oceanside (Atlantic Ocean) wet; B = bay (Florida Bay) wet; D = oceanside dry; T = all treatments combined.

posure periods up to 1 h resulted in corresponding increases in mortality. Similar mortality has been observed in the Western Australia spiny lobster (*Panulirus cygnus*) fishery (Brown and Caputi 1983; Brown et al. in press). In that fishery, undersize lobsters are not used as bait but are often retained aboard vessels for varying periods during the sorting process. To test effects of that practice, Australian lobsters were tagged, held aboard vessels for 0, ¼, ½, 1, and 2 h, and then released. Recapture rates were markedly lower in exposed groups than in controls. As in our experiments, results from exposure times >1 h were similar to those of 1 h exposures.

The greatest rate of mortality to *Panulirus argus* in our tests occurred during the first week following exposure (Fig. 2). Although physiological causes of mortality have not been determined, several factors may be involved. Dehydration due to desiccation may affect survival, but lobsters dampened at ½ h intervals died at rates similar to those left unattended. One effect of exposure is to dry gills (Anonymous 1980), which may result in respiratory problems. Dehydration and gill damage may cause mortality directly, but more likely are contributory factors to physiological stress caused by buildup of toxic compounds in the blood. Handling stress has been demonstrated to cause temporary acidic conditions in the blood of European lobsters, *Homarus vulgaris* (McMahon et al. 1978). After reimmersion in seawater, lobsters should rehydrate fairly quickly, but effects of physiological stress are likely to linger.

Contrary to prior expectations, mortality rates of dampened lobsters did not differ significantly from those left unattended (dry). Dampening also failed to enhance survival of the northern lobster, *Homarus americanus* (McLeese 1965). McLeese suggested that a relationship existed between metabolic rate and mortality. An increase in metabolic rate and concurrent more rapid depletion of reserves may have offset advantages of increasing moisture by dampening during our experiments as well.

Exposure was probably the principal cause of mortality among bait lobsters during our tests in Florida Bay. However, a small but distinctly greater level of mortality among all lobsters, including controls during weeks 1-3 and a marked increase in mortality during week 4 at the ocean site, suggest that other factors in addition to exposure were responsible for mortalities there (Figs. 1, 2). When average mortality rates of controls (Table 1) are subtracted from overall average mortality rates of exposed lobsters, resultant values (18.6%, Florida Bay; 18.3%, Atlantic reefs) are nearly equal and probably represent the rates of mortality actually ascribable to exposure at each site. Thus, effects of exposure were similar regardless of where traps were placed.

Mortality due to other effects related to confinement evidently do vary depending upon locations where traps are placed, especially if confinement periods are lengthy. Increased mortality rates such as those we observed during week 4 at the Atlantic reef site may result from starvation. Lyons and Kennedy (1981) presented evidence of weight loss and starvation among lobsters confined at densities of 3 and 5/trap in Florida Bay for 8 wk. Rate of weight loss increased during week 4 among lobsters at densities of 5 but did not increase rapidly until week 6 among lobsters confined at densities of 3. Those tests were conducted in the same portion of Florida Bay where present exposure tests were conducted, an area characterized by muddy sand overlain by seagrass beds. A disparity in available food organisms between this area and that where oceanside tests were conducted may explain differences in mortality during week 4.

Seagrass beds in Florida Bay are lush and heavily covered with epibionts (J. H. Hunt, pers. obs.). These epibionts serve as food for larger organisms which in turn are appropriate food for *Panulirus argus*. Snails in the genera such as *Modulus*, *Turbo*, *Astraea*, and *Cerithium* and crabs in the genera *Mithrax* and *Pitho* are abundant in these grass beds and are frequently seen within or clinging to sides of lobster traps. All of these also occur commonly in stomach contents of *P. argus* in south Florida (W. G. Lyons, pers. obs.). At the ocean site, grass beds are sparse and patchily distributed, and fewer organisms enter traps from the surrounding sand. It seems reasonable to suppose that the weight loss observed to occur among lobsters confined near lush

TABLE 3.—Results of Wilcoxon Two Sample Tests (*Z* values) from comparisons of mean weekly (1-4) mortality rates for various treatments at Florida Bay (Bay) and Atlantic Reef (Ocean) locations.

Tests	Week	1	2	3	4
Bay wet	1	—			
	2	2.86**	—		
	3	2.40*	0.55	—	
	4	3.58***	0.94	1.48	—
Ocean wet	1	—			
	2	2.72**	—		
	3	3.04**	0.59	—	
	4	0.66	2.08*	2.50*	—
Ocean dry	1	—			
	2	2.40*	—		
	3	3.33***	1.02	—	
	4	1.31	1.14	2.13*	—

* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$.

grass beds (Lyons and Kennedy 1981) might occur at accelerated rates in the relatively more sparse ocean environment. If food is sufficiently scarce, accelerated weight loss may lead to starvation and increased mortality within the observed 4-wk period.

Traps in these experiments had their entrances boarded over to prevent escape, whereas lobsters that escape from traps used in the fishery are likely to recover from effects of starvation. Escape rates, though, are quite low, ranging from 0.8 to 1.8%/d (Yang and Obert 1978; Davis and Dodrill 1980; Lyons and Kennedy 1981).

We offer no explanation for our observation that highest mortality rates are associated with 1-h exposures nor for the persistent background mortality among oceanside controls. Nevertheless, neither seem to be artifacts of experimental design and, instead, probably represent other yet-to-be understood physiological reactions to stress caused by exposure, handling, or confinement. If so, they represent other effects of baiting with shorts and are justly included among estimates of total fishery-induced mortality.

Economic Effects of Mortality

Baiting traps with shorts results in significant economic loss to the fishery. Although use of shorts is an effective means of attracting other lobsters without requiring out-of-pocket expenses for bait, each bait lobster that dies is one that potentially will not enter fishery landings. In addition, repair of broken legs, antennae, and other injuries caused by handling may retard growth by as much as 40% (Davis 1981), increasing the time required for a lobster to attain legal size and extending the time during which it may be used as bait. An injured lobster that escapes from a trap where it was placed will direct energy toward repair, not growth, thereby reducing the probability that it will attain legal size during its next molt. If the lobster does not attain legal size, it is again vulnerable to capture and to use as bait. Confinement itself also results in reduced lobster growth rate (Kennedy 1982), which doubtlessly extends the period during which a lobster may be vulnerable to use as bait.

The hidden costs of baiting with shorts needs to be considered in future management efforts. The following model, based only upon observed mortality rates, estimates that cost:

$$Y = A \times B \times C \times D$$

where Y = seasonal mortality of shorts used as bait;
A = number of traps in the fishery;
B = average number of shorts per trap;
C = season length (in months);
D = average monthly mortality rate.

Because the actual allocation of fishery traps among Florida Bay and Atlantic sites is unknown but believed to be relatively equal, we selected the unweighted average cumulative 4-wk mortality rate to estimate monthly mortality throughout the fishery. By using a range of values for other variables, several estimates of the average number of shorts that die seasonally because of fishery baiting practices may be obtained (Table 4). Thus, if each trap in the fishery is baited with only 1 short/mo and all fishermen leave the fishery after only 4 mo, more than 600,000 sublegal lobsters may die as a result of their use as bait. If all traps are deployed for the full 8 mo and each trap uses 3 shorts as bait, more than 3.6 million shorts may die as a result of that use. Both examples probably represent extreme cases, and actual fishery-induced mortality probably lies somewhere between these estimates.

The problem is really more complex. Some lobsters that die because they were used as bait would probably fall victim to other causes, but natural mortality among lobsters of sizes appropriate for use as bait (65-75 mm CL) may be low, particularly since incidence of their principal predators, large serranids, has been greatly reduced in the fishery area. Furthermore, not all traps are baited with shorts because shorts are not readily available in some peripheral areas of the fishery. Both of these factors suggest that the model may overestimate fishery-induced mortality. However, values used in the model for numbers of shorts per trap are probably low. Fishermen prefer to use 3-5 shorts/trap (Gulf of Mex-

TABLE 4.—Estimates of the economic effect of baiting with shorts in the south Florida spiny lobster fishery.

Average monthly mortality rate[1]	No. of traps in fishery[2]	Season length[3]	No. of shorts/ trap[4]	Seasonal mortality of shorts as bait
0.263	573,000	4	1	602,796
0.263	573,000	4	3	1,808,338
0.263	573,000	6	1	904,194
0.263	573,000	6	3	2,712,582
0.263	573,000	8	1	1,205,592
0.263	573,000	8	3	3,616,776

[1]Unweighted average cumulative 4-wk mortality rate from this study.
[2]Number of traps in 1981 (E. J. Little, Jr., Southwest Fisheries Center Resource Statistics Office, National Marine Fisheries Service, NOAA, P.O. Box 269, Key West, FL 33041, pers. commun. November 1982).
[3]The season is 26 July-31 March, 8+ mo; some fishermen begin removing their traps after November, and many have left the fishery by the end of January, causing a considerable reduction in the number of traps fished during February and March.
[4]Conservative estimates; fishermen try to put as many shorts as available into traps.

ico and South Atlantic Fishery Management Councils 1982), and it seems probable from fishermen's comments that virtually no shorts are intentionally released. Similarly, the model only allows one input of bait per month, whereas in reality additional shorts are continually introduced, typically at 1-2 wk intervals, to replace others lost because of death or escape. These factors suggest that the model may underestimate fishery-induced mortality.

Regardless of which values are applied, the model indicates that resultant losses to the fishery are considerable. Since a lobster weighs slightly <1 lb at legal size, fishery-induced mortality may cause losses ranging from 0.6 to 3.6 million lb. At recent ex-vessel prices of $2.50 per pound, this represents a potential loss to the fishery of $1.5-$9.0 million annually. In 1981, total reported commercial lobster harvest was 5.9 million lb valued at $14.5 million[3], so the hidden cost of baiting with shorts is considerable.

This loss may be viewed as a necessary cost, albeit large, of doing business in the fishery or as a problem that may be alleviated by alternative management strategies. If the latter course is deemed necessary, use of other baits and installation of escape gaps that allow shorts to escape while retaining legal lobsters in traps (Bowen 1963) are potentially effective strategies to increase harvest of legal lobsters without adversely affecting the population.

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[3]Statistical Surveys Branch. 1983. Florida landings 1981. Southeast Fisheries Center National Statistical Office, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149.

LITERATURE CITED

ANONYMOUS.
1980. The fate of undersized rock lobsters returned to the sea. West. Aust. Dep. Fish. Wildl., Fish. Ind. News Serv. (F.I.N.S.) 13:10-12.

BOWEN, B. K.
1963. Management of the western rock lobster, (*Panulirus longipes cygnus* George). Proc. Indo-Pac. Fish. Counc. 14: 139-154.

BROWN, R. S., AND N. CAPUTI.
1983. Factors affecting the recapture of undersize western rock lobster *Panulirus cygnus* George returned by fishermen to the sea. Fish. Res. 2:103-128.

BROWN, R. S., J. PRINCE, N. CAPUTI, AND J. JERKE.
In press. Fishery induced mortality of undersize western rock lobster. West. Aust. Dep. Fish. Wildl. Bull.

COPE, C. E.
1959. Spiny lobster gear and fishing methods. U.S. Fish Wildl. Serv., Fish. Leafl. 487, 17 p.

DAVIS, G. E.
1981. Effects of injuries on spiny lobster, *Panulirus argus*, and implications for fishery management. Fish. Bull., U.S. 78:979-984.

DAVIS, G. E., AND J. W. DODRILL.
1980. Marine parks and sanctuaries for spiny lobster fishery management. Proc. Gulf Caribb. Fish. Inst. 32:194-207.

GULF OF MEXICO AND SOUTH ATLANTIC FISHERY MANAGEMENT COUNCILS.
1982. Fishery management plan, environmental impact statement and regulatory impact review for spiny lobster in the Gulf of Mexico and South Atlantic. Gulf of Mexico and South Atlantic Fishery Management Councils, Tampa, Fla., var. p.

KENNEDY, F. S., JR.
1982. Catch rates of lobster traps baited with shorts, with notes on effects of confinement. *In* W. G. Lyons (editor), Proceedings of a workshop on Florida spiny lobster research and management, p. 20. Fla. Dep. Nat. Resour. Mar. Res. Lab., St. Petersburg.

LYONS, W. G., D. G. BARBER, S. M. FOSTER, F. S. KENNEDY, JR., AND G. R. MILANO.
1981. The spiny lobster, *Panulirus argus*, in the middle and upper Florida Keys: population structure, seasonal dynamics, and reproduction. Fla. Mar. Res. Publ. 38, 38 p.

LYONS, W. G., AND F. S. KENNEDY, JR.
1981. Effects of harvest techniques on sublegal spiny lobsters and on subsequent fishery yield. Proc. Gulf Caribb. Fish. Inst. 33:290-300.

MCLEESE, D. W.
1965. Survival of lobsters, *Homarus americanus*, out of water. J. Fish. Res. Board Can. 22:385-394.

MCMAHON, B. R., P. J. BUTLER, AND E. W. TAYLOR.
1978. Acid base changes during recovery from disturbance and during long term hypoxic exposure in the lobster, *Homarus vulgaris*. J. Exp. Zool. 205:361-370.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Co., San Franc., 776 p.

WOLFFERTS, R. C.
1974. Fishermen's problems in the spiny lobster fishery. *In* W. Seaman, Jr., and D. Y. Aska (editors), Conference proceedings: Research and information needs of the Florida spiny lobster fishery, p. 3 [abstr.], 8, 9. Fla. Sea Grant Rep. SUSF-SG-74-201, Gainesville, FL.

YANG, M. C. K., AND B. OBERT.
1978. Selected statistical analyses of Key West spiny lobster data. *In* R. E. Warner (editor), Spiny lobster research review; proceedings of a conference held December 16, 1976 in Key West, Florida, p. 4-7. Fla. Sea Grant Tech. Pap. No. 4.

TYPE, QUANTITY, AND SIZE OF FOOD OF PACIFIC SALMON (*ONCORHYNCHUS*) IN THE STRAIT OF JUAN DE FUCA, BRITISH COLUMBIA

TERRY D. BEACHAM[1]

ABSTRACT

The volume, numbers, and size of prey of sockeye, *Oncorhynchus nerka*; pink, *O. gorbuscha*; coho, *O. kisutch*; and chinook, *O. tshawytscha*, salmon were investigated for troll-caught salmon in the Strait of Juan de Fuca off southwestern Vancouver Island during 1967-68. Sockeye salmon was the least piscivorous species with only 7% of the stomach volume comprised of fish, while chinook salmon was the most piscivorous species at 56%. Sand lance, *Ammodytes hexapterus*, and euphausiids were the most important fish and invertebrate prey, respectively. As predator size increased, mean size of fish prey increased, and predators shifted to species of larger mean size. Similar results were found for the invertebrate prey, with mean number of prey consumed per predator increasing for the larger invertebrate species as predator size increased. Rate of increase in mean length of fish prey was proportional to increasing predator length. The observed increase in invertebrate size with increasing predator length was not statistically significant. Although chinook and coho salmon had similar diets, they were caught at significantly different water depths. *Oncorhynchus* species with fewer, shorter, and more widely spaced gillrakers have higher proportions of fish in their diet than species with numerous, long, and narrow set gillrakers.

The life history of Pacific salmon is quite variable among species, with fry of pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *O. keta*, migrating to sea soon after emergence from the gravel, while those of sockeye salmon, *O. nerka*, coho salmon, *O. kisutch*, and chinook salmon, *O. tshawytscha*, may spend up to 2 yr in freshwater. Once in the ocean they can migrate a considerable distance from their natal streams and feed on a variety of organisms (Godfrey et al. 1975; French et al. 1976; Major et al. 1978; Takagi et al. 1981). Salmon thus move through a number of habitats during their life cycle and consume a diverse array of prey.

Food preferences of salmon in the range of habitats that they occupy have been an area of continuing investigation (Allen and Aron 1958; Prakash 1962; LeBrasseur 1966; Parker 1971; Eggers 1982). Relative amounts of different prey types eaten in varying environments have been examined, as well as preferences by different sizes of predators in relation to the size and abundance of prey. *Oncorhynchus* species differ considerably in their size, morphology, and ocean distribution (Hikita 1962; Neave et al. 1976; Takagi et al. 1981; Beacham and Murray 1983). Morphological differences and diet partitioning have been reported for many fish species (Keast and Webb 1966; Hyatt 1979), and diet partitioning may thus be expected among *Oncorhynchus* species. Prey size is related to predator size (O'Brien 1979; Gibson 1980), and differential prey selection among *Oncorhynchus* species may also be apparent.

Stomach contents of sockeye, pink, coho, and chinook salmon were investigated in a research trolling program conducted off southern Vancouver Island in the Strait of Juan de Fuca during 1967-68. The relative importance of different prey types, including fish and invertebrates, in the diet of the four species was studied with respect to prey size, predator size, predator morphology, and diet partitioning in relation to salmonid habitat and morphology.

MATERIALS AND METHODS

The salmon were obtained by test trolling in the Strait of Juan de Fuca during 19 June-11 October 1967 and 1 May-12 July 1968 (Fig. 1). Detailed methodology of the program has been outlined by Graham and Argue (1972). For each salmon sampled, date, fork length (mm), round weight, and sex were recorded. Stomachs were removed, placed in numbered cloth sample bags along with any food organisms in the mouth cavity, and preserved in 10% Formalin[2] solution.

[1]Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, British Columbia V9R 5K6, Canada.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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FIGURE 1.—Location of study area in Strait of Juan de Fuca off southwestern Vancouver Island.

Laboratory analysis involved sorting the contents into the classifications outlined in Table 1 by using a low-power binocular microscope. Numbers of organisms in each classification were recorded, if possible, for each individual salmon. Once individuals were counted, displacement volumes (mL) were determined separately for fish contents, for crustacean contents, and for miscellaneous organisms. If organisms were too digested to assign to individual classifications but could be identified as fish or crustaceans, their volumes were included in either the unidentified fish volume or unidentified crustacean volume classification.

Two techniques of data analysis were used.

TABLE 1.—Percentage of salmon sampled with empty stomachs and average number of prey per fish with non-empty stomachs.

			Prey type										
Class	*N*	% empty	Sand lance	Herring	Rockfish (*Sebastes*)	Other fish	Euphausiids	*Parathemisto*	Crab larvae	Mysids	Amphipods*	Crabs	Miscellaneous crustaceans
Sockeye <55 cm	22	46	—	—	—	—	3.7	13.2	5.0	0.3	—	—	0.1
Sockeye >55 cm	117	41	0.2	—	—	—	13.5	8.6	0.4	0.1	—	—	0.4
Total	139	42	0.2	—	—	—	12.1	9.3	1.1	0.1	—	—	0.4
Pink <55 cm	301	26	0.7	—	—	—	9.7	13.7	1.0	0.3	—	0.1	0.3
Pink >55 cm	498	32	0.4	—	—	0.1	15.3	13.1	2.4	0.1	0.1	0.1	0.4
Total	799	30	0.5	—	—	0.1	13.1	13.3	1.9	0.2	0.1	0.1	0.4
Coho <40 cm	1,045	49	0.4	—	—	0.2	6.3	1.2	0.4	1.3	0.1	0.2	0.3
Coho 40-60 cm	1,039	28	5.8	—	0.1	0.3	29.8	0.3	0.9	0.3	—	0.2	0.4
Coho >60 cm	130	32	0.5	0.2	—	—	51.0	0.4	0.6	—	—	—	0.6
Total	2,214	38	3.3	—	—	0.2	22.1	0.7	0.7	0.6	—	0.2	0.4
Chinook <40 cm	607	39	1.1	—	—	0.1	5.4	0.1	0.7	0.4	—	—	0.7
Chinook 40-60 cm	786	36	1.6	0.1	—	0.1	15.3	0.2	0.2	0.6	—	—	0.1
Chinook >60 cm	83	47	0.8	0.3	—	—	62.4	—	0.4	0.1	—	—	—
Total	1,476	38	1.4	0.1	—	0.1	13.6	0.1	0.4	0.5	—	—	0.3

*Other than *Parathemisto*.

Methodology for the first, percent occurrence of each of the prey types, has been outlined by Hynes (1950). All chi-square tests in the analysis for frequency of occurrence of prey types have one degree of freedom. The second technique involved determining percentage by volume of total stomach contents for fish, crustaceans, miscellaneous organisms, and also for the individual prey classifications. Fish, crustaceans, and miscellaneous organisms were recorded by volume, and thus determining percentage of total stomach volume for each classification was direct. For individual prey types, it was necessary to convert numbers of individual organisms to volumes by calculating the volume displaced by a single organism of each prey type. This was done by selecting individual salmon of each species with only one fish and/or one crustacean prey type in the stomach. The unit volumes for each prey type were then calculated as the sum of the fish or crustacean volumes for the selected fish divided by the number of the prey type under consideration. If there was only one unknown in the stomach contents with prey of known (calculated) volumes (the number of prey types multiplied by their unit volumes), the total volume of known prey was subtracted from the total fish or crustacean volume until only one unknown prey class remained. Then the volume of the prey class in question was obtained and its unit volume calculated. Comparisons of prey size among the species were analyzed by analysis of variance.

For an individual salmon with more than one fish or one crustacean prey class in its stomach, volume of each prey class was determined by multiplying the number of organisms by their unit volume. This total volume obtained was scaled proportionately so that individual components when summed equalled the total known fish or crustacean volume.

RESULTS

Volume and Frequency of Food Items

For each species, over 30% of the individuals had empty stomachs (Table 1). In comparing fish with non-empty stomachs, sockeye salmon was the least piscivorous, with a mean 7% fish component in the diet (Fig. 2). In sockeye salmon <55 cm fork length (FL), only 2% of the stomach volume was comprised of fish. At 17% of total food volume, fish was a greater dietary component of pink salmon than of sockeye (Fig. 2). However, the fish component of the diet of sockeye and pink salmon was considerably less than that of coho (46%) and chinook (56%) salmon. Fish comprised 30% of the stomach content volume of coho <40 cm FL, but almost 50% of the stomach content volume of larger coho. Chinook salmon was the most piscivorous of the four species, and the 56% fish component of the diet was constant for the three size classes of chinook salmon investigated, although the species composition of the fish prey changed.

The relative importance of individual prey types was investigated for the four salmon species. Sand lance, *Ammodytes hexapterus*, was virtually the sole fish component of the diet of sockeye salmon, occurring in 4% of the 81 non-empty sockeye salmon stomachs sampled (Fig. 3). Euphausiids were the most important prey for sockeye, occurring in 58% of non-empty stomachs and comprising 71% of the total volume of food eaten. The hyperiid amphipod *Parathemisto* comprised over 11% of the volume of food eaten. Of the fish prey species, sand lance was again the most important for pink salmon, occurring in 9% of 562 non-empty stomachs and comprising 10% of total stomach contents (Fig. 4). There was no significant difference between sockeye and pink salmon in the frequency of occurrence of sand lance in their diets ($\chi^2 = 2.65$, $P > 0.05$). Fish species other than sand lance (herring, *Clupea harengus*, and rockfish, *Sebastes* sp.) comprised less than 1% of stomach contents of pink salmon. As in sockeye salmon, the dominant invertebrate prey types were euphausiids at 62% of stomach content volume and *Parathemisto* at 14%. Frequency of occurrence of euphausiids ($\chi^2 = 1.63$, $P > 0.05$) and *Parathemisto* ($\chi^2 = 3.54$, $P > 0.05$) were similar for sockeye and pink salmon.

Fish species were a significant food for coho and chinook salmon. For example, sand lance occurred in 27% of 1,364 non-empty stomachs of coho salmon, and also comprised 27% of total stomach volume (Fig. 5). Herring comprised <1% of the stomach content volume of coho <40 cm FL, but 25% of the volume for coho >60 cm FL. The dominant invertebrate prey type was euphausiids, comprising 51% of total stomach contents, while all invertebrate prey types combined comprised only 54%. The relative importance of fish as a prey type was greatest in chinook salmon, with sand lance again the dominant prey species, occurring in 34% of 914 non-empty stomachs, and comprising 35% of total volume of contents (Fig. 6). Sand lance occurred in the diet of chinook and coho salmon at similar frequencies ($\chi^2 = 0.80$, $P > 0.05$), as did herring ($\chi^2 = 0.08$, $P > 0.05$). Herring comprised 9% of the stomach contents for chinook salmon <40 cm FL, but 33% of the stomach contents for chinook salmon >60 cm FL.

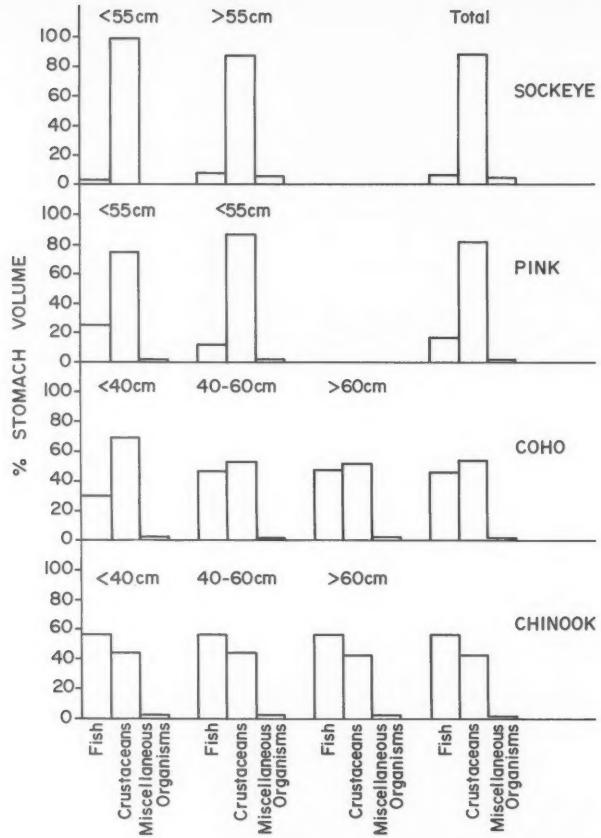

FIGURE 2.—Percentage volumes of stomach contents of the fish, crustacean, and miscellaneous organism component for sockeye, pink, coho, and chinook salmon sampled in Strait of Juan de Fuca during 1967-68.

Coho ate greater numbers of fish than did chinook salmon (Table 1), but chinook had a greater volume of the stomach contents composed of fish (56% chinook, 46% coho). This result suggests chinook eat larger fish than coho (Table 2). As with coho, euphausiids were the dominant invertebrate prey type of chinook salmon, comprising 40% of a total invertebrate volume of 44% of stomach contents. However, euphausiids occurred significantly more often in the diet of coho salmon than in chinook salmon ($\chi^2 = 4.73$, $P < 0.01$).

Fish were a more significant dietary component of chinook and coho salmon than of sockeye and pink salmon. Sand lance occurred significantly more often in the diet of chinook and coho salmon than in the diet of sockeye and pink salmon ($\chi^2 = 152.9$, $P < 0.01$). Similar results were also found for herring ($\chi^2 = 18.1$, $P < 0.01$), rockfish ($\chi^2 = 7.2$, $P < 0.01$), and mixed fish species ($\chi^2 = 39.0$, $P < 0.01$). Invertebrate prey were more significant in the diet of sockeye and pink salmon than in that of chinook and coho. Euphausiids occurred more frequently in the diet of sockeye and pink salmon ($\chi^2 = 199.3$, $P < 0.01$), as did *Parathemisto* ($\chi^2 = 619.5$, $P < 0.01$), crab larvae ($\chi^2 = 171.1$, $P < 0.01$), and amphipods ($\chi^2 = 9.2$, $P < 0.01$). There was no difference in frequency of occurrence of crabs in the diet ($\chi^2 = 0.01$, $P > 0.05$) which occurred only at low levels or not at all, but mysiids occurred more frequently in the diet of chinook and coho salmon than in

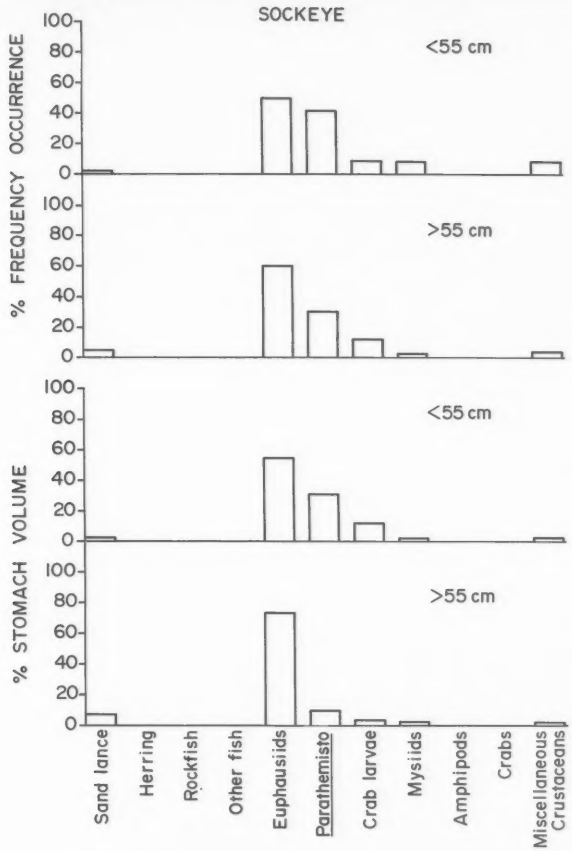

FIGURE 3.—Percentage frequency of occurrence and percentage stomach volume of prey types listed in Table 1 for sockeye salmon.

that of sockeye and pink salmon ($\chi^2 = 36.0$, $P < 0.01$).

Predator and Prey Size

The effect of predator size on the abundance and size of prey was examined for each of the four salmon species investigated. Numbers of individuals consumed for each prey type were tallied for each salmon examined. For the fish prey species, only sand lance was consumed at a high enough frequency to enable one to investigate numbers of sand lance consumed versus predator size. For the four salmon species, there was no consistent trend for sand lance in this regard (Table 1). For both chinook and coho salmon—the two primary sand lance predators—the number of sand lance eaten was greater in the middle size group than in either the small or large size classes. Large chinook and coho salmon switched from sand lance to larger fish species, such as herring (Figs. 5, 6). There were, however, clear trends for some of the invertebrate prey types. The average number of euphausiids eaten per individual predator increased with increasing fish size (Table 1). However, the average number of *Parathemisto* eaten decreased with increasing predator size. The other prey types occurred at a low frequency (Figs. 3-6), and thus it was not possible to determine reliable trends.

As predator size increased, more euphausiids, but

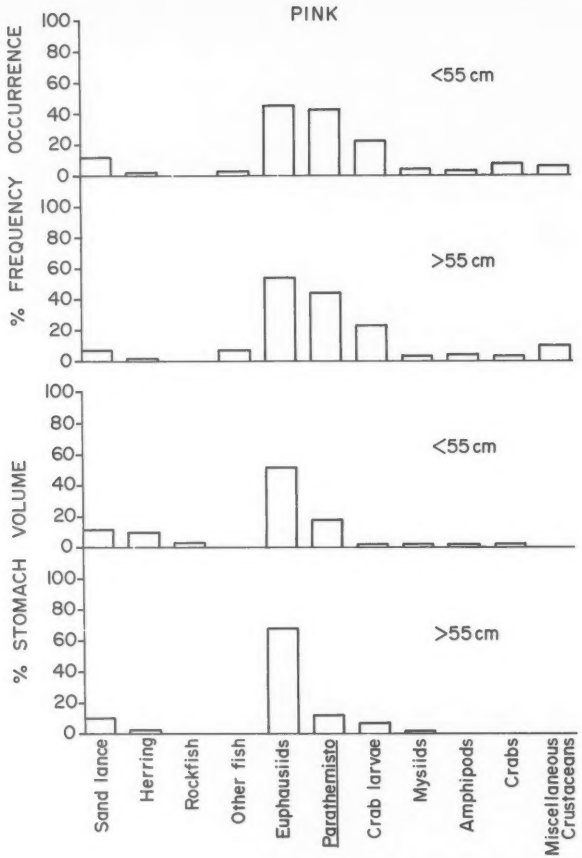

FIGURE 4.—Percentage frequency of occurrence and percentage stomach volume of prey types for pink salmon.

less *Parathemisto*, were eaten per individual predator. The difference in predator response to euphausids and *Parathemisto* may be examined in relation to the size of the prey. The unit volumes of an individual euphausiid were about four times larger than those of an individual *Parathemisto* (Table 2). In each salmon species examined, as the predators increased in size, they switched from the smaller *Parathemisto* to the larger euphausiids and also crab larvae, consuming greater numbers of the larger prey and decreasing numbers of the smaller prey. Chinook and coho salmon also consumed significantly larger *Parathemisto* than did sockeye and pink salmon ($F = 4.9$; df = 3,98; $P < 0.01$). For the invertebrate prey, an increase in predator size resulted in greater numbers of larger prey being consumed.

As predator size increased, there was an increase in the size of the prey consumed (Table 2). Larger predators consumed larger sand lance and herring. Chinook and coho salmon consumed larger sand lance ($F = 3.7$; df = 3,613; $P < 0.05$) and mixed fish species ($F = 2.9$; df = 2,128; $P < 0.05$) than did sockeye and pink salmon. In coho and chinook salmon, there was also a tendency for larger salmon to switch prey types from the smaller sand lance to the larger herring and rockfish. Increasing predator size produced shifts in both the type, number, and size of the prey consumed.

Changes in size of prey and predators were in-

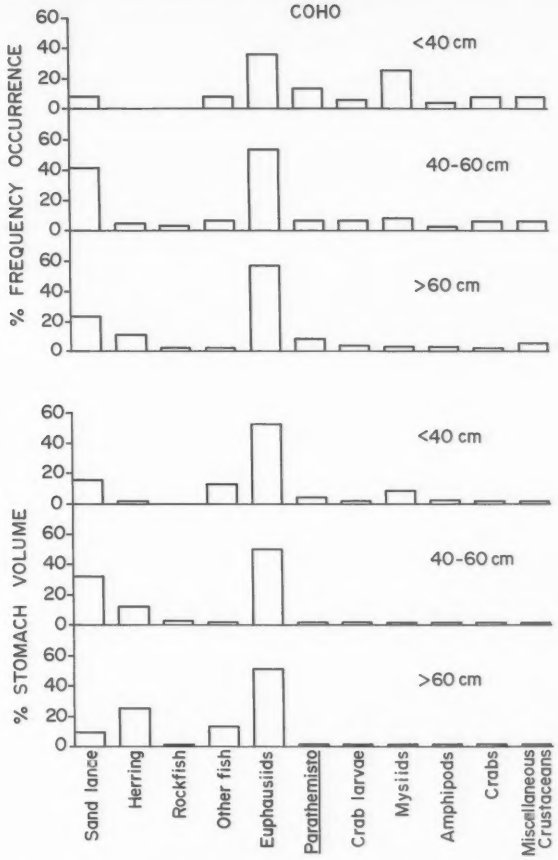

FIGURE 5.—Percentage frequency of occurrence and percentage stomach volume of prey types for coho salmon.

vestigated for the two most frequently occurring fish prey (sand lance, herring) and crustacean prey (euphausiids, *Parathemisto*). Size classes for sockeye and pink salmon were below and above 55 cm FL, and those for chinook and coho salmon below and above 60 cm FL. I assume that the value of the cube root of the volume ratio of the prey is proportional to the prey length ratio, and thus changes in prey size can be compared with changes in predator size.

Mean size of the fish component of the prey increased as predator size increased (Table 3). As the size of pink, coho, and chinook salmon increased by 13%, 65%, and 69%, respectively, the size of the sand lance consumed increased by 16%, 83%, and 83%, respectively. The size of herring eaten also increased as predator size increased, and for pink and chinook salmon it was about equal to the increase in size of the predator species. When the predator responses to increase in size of both prey species are pooled, there is a weak correlation between increasing predator length and increasing prey length ($r = 0.69$, $n = 6$, $P > 0.05$); but if the coho salmon response to increasing herring size is deleted, the relationship is much stronger between increasing predator and prey size ($r = 0.98$, $n = 5$, $P < 0.01$).

Apparent trends of invertebrate prey size with predator size were not statistically significant. For sockeye and pink salmon, mean size of individuals in the two invertebrate prey classes decreased as

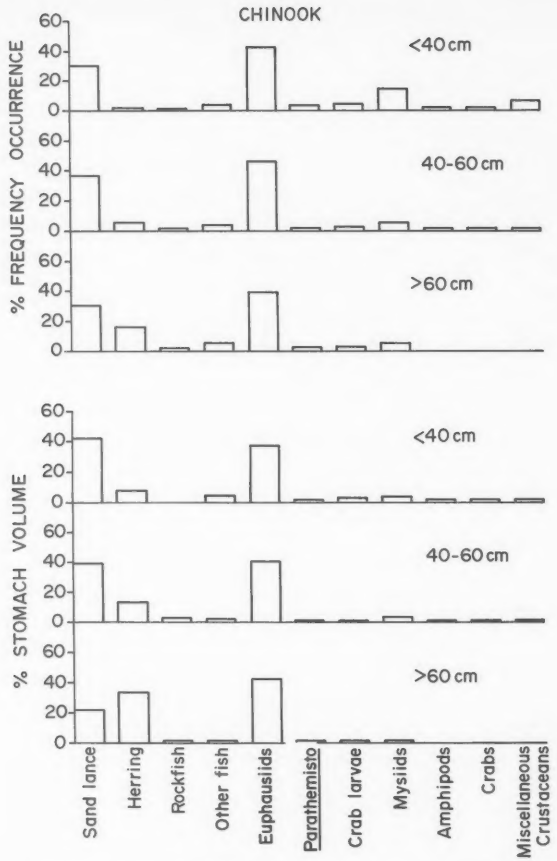

FIGURE 6.—Percentage frequency of occurrence and percentage stomach volume of prey types for chinook salmon.

predator size increased, but not significantly (Table 3) ($r = -0.24$, $n = 4$, $P > 0.05$). For chinook and coho salmon, mean size of the invertebrate prey increased as predator size increased ($r = 0.42$, $n = 4$, $P > 0.05$). However, the increase in prey size was considerably less than the increase in predator size (Table 3).

The results of the previous analyses are summarized as follows. As predator size increased, individual predators selected larger fish prey of one species, but not a greater number of the prey. There was also a shifting from smaller prey species (sand lance) to larger ones (herring, rockfish). As predator size increased, there was a tendency to shift from smaller invertebrate prey (*Parathemisto*) to larger types (euphausiids, crab larvae). Greater numbers of the larger prey were consumed by an individual predator, while numbers of smaller prey consumed declined. Although larger invertebrate prey types were preferred as predator size increased, larger individuals of each prey class were not necessarily selected by larger predators.

Species Comparisons

The dietary components of the four species of salmon investigated are different, and there is more than one possible reason for the apparent partitioning of diet among the salmon species. Perhaps because the salmon occupied different depth zones, the differences in diet are attributable simply to dif-

TABLE 2.—Calculated mean volumes (ml) per individual for prey organisms. These va
are in parenthes

Class	Sand lance	Herring	Rockfish (*Sebastes*)	Other fish	Euphausiids	
Sockeye						
<55 cm	—	—	—	—	1.24 (4)	0.18
>55 cm	3.18 (3)	—	—	—	0.81 (29)	0.13
Total	3.18 (3)	—	—	—	0.86 (33)	0.14
Pink						
<55 cm	3.01 (24)	90.00 (4)	26.00 (1)	4.50 (6)	1.17 (85)	0.27
>55 cm	4.75 (20)	120.00 (1)	—	1.68 (18)	0.98 (156)	0.57
Total	3.80 (44)	96.00 (5)	26.00 (1)	2.39 (24)	1.05 (241)	0.21
Coho						
<40 cm	4.33 (38)	32.50 (2)	—	7.36 (40)	1.27 (161)	0.46
40-60 cm	4.40 (289)	170.34 (24)	21.32 (9)	3.39 (36)	1.33 (349)	0.42
>60 cm	26.98 (19)	207.50 (10)	12.00 (1)	888.00 (1)	1.44 (48)	0.60
Total	5.63 (346)	173.00 (36)	20.39 (10)	16.94 (77)	1.32 (558)	0.45
Chinook						
<40 cm	6.09 (106)	57.71 (5)	16.00 (1)	10.08 (14)	1.28 (130)	0.20
40-60 cm	9.88 (169)	51.56 (22)	37.00 (6)	6.31 (17)	1.14 (190)	0.38
>60 cm	51.40 (12)	245.45 (7)	30.00 (1)	1.00 (1)	1.40 (16)	0.55
Total	10.22 (287)	92.38 (34)	33.50 (8)	7.79 (32)	1.21 (336)	0.30

hese values were used to convert prey numbers to prey volumes. Sample sizes rentheses.

Parathemisto	Crab larvae	Mysiids	Amphipods	Crabs	Miscellaneous crustaceans
0.18 (3)	0.17 (1)	—	—	—	—
0.13 (8)	1.00 (2)	2.86 (1)	—	—	0.07 (2)
0.14 (11)	0.72 (3)	2.86 (1)			
0.27 (48)	0.30 (8)	0.93 (4)	1.00 (1)	—	—
0.57 (68)	0.57 (18)	0.50 (4)	1.17 (1)	0.50 (4)	0.30 (7)
0.21 (116)	0.49 (26)	0.72 (8)	1.09 (2)	0.50 (4)	0.30 (7)
0.46 (37)	0.35 (13)	1.00 (86)	0.90 (12)	0.71 (18)	0.19 (95)
0.42 (20)	0.64 (17)	2.31 (30)	1.43 (7)	0.86 (18)	0.38 (7)
0.60 (2)	1.00 (2)	2.00 (1)	3.67 (3)	0.33 (1)	1.00 (2)
0.45 (59)	0.54 (32)	1.34 (117)	1.45 (22)	0.77 (37)	0.22 (104)
0.20 (2)	0.55 (8)	1.29 (37)	2.14 (5)	0.70 (2)	0.13 (10)
0.38 (7)	0.31 (8)	2.11 (21)	2.00 (1)	1.00 (1)	4.11 (3)
0.55 (1)	0.68 (1)	2.20 (2)	—	—	—
0.36 (10)	0.44 (17)	1.66 (58)	2.12 (6)	0.80 (3)	1.05 (13)

TABLE 3.—Mean lengths (cm) of salmon and mean size of prey. Mean lengths of sockeye and pink salmon were for those in the size classes below (L_1) and above (L_2) 55 cm, whereas those for coho and chinook salmon were those below (L_1) and above (L_2) 60 cm. The prey ratio $\sqrt[3]{V_2/V_1}$ is assumed to be indicative of ratios in prey lengths between the two groups of predators. The two most frequent fish and invertebrate prey species listed are euphausiids (EU), *Parathemisto* (PA), sand lance (SL), and herring (HR).

Predator				Prey				
	Mean length		$\frac{L_2}{L_1}$	Prey	Mean volume		$\frac{V_2}{V_1}$	$\sqrt[3]{\frac{V_2}{V_1}}$
Species	L_1	L_2		types	V_1	V_2		
Sockeye	50.7	58.7	1.16	EU	1.24	0.81	0.65	0.87
				PA	0.18	0.13	0.72	0.90
Pink	51.8	58.5	1.13	SL	3.01	4.75	1.58	1.16
				HR	90.00	120.00	1.33	1.10
				EU	1.17	0.98	0.84	0.94
				PA	0.27	0.17	0.62	0.86
Coho	40.0	65.8	1.65	SL	4.39	26.98	6.15	1.83
				HR	159.73	207.50	1.30	1.09
				EU	1.31	1.44	1.10	1.03
				PA	.45	.60	1.33	1.10
Chinook	41.2	69.5	1.69	SL	8.42	51.4	6.10	1.83
				HR	52.70	245.45	4.66	1.67
				EU	1.20	1.40	1.17	1.05
				PA	0.34	0.55	1.61	1.17

ferences in prey abundances by depth. The numbers of salmon caught with non-empty stomachs were tabulated by depth zone of capture (Table 4). Coho salmon were most abundant in water depths of <18 m, whereas sockeye and pink salmon were most abundant between depths of 18 and 36 m, and chinook salmon most abundant in depths >18 m. Coho and chinook salmon have similar diets, but are found at significantly different depths ($\chi^2 = 714.7$, $P < 0.01$). Thus partitioning of the diets among salmon species is not related simply to water depth.

Morphological characters of the salmon species were compared with their food preferences. Chinook and coho salmon have fewer, shorter, and more widely spaced gillrakers than those of sockeye and pink salmon (Table 5). As gillrakers are used to strain food organisms from water passing over the gills (Lagler et al. 1962), I expected salmon species feeding on planktivorous prey to have more gillrakers that are longer and more closely set than those in primarily piscivorous salmon species. Similar arguments could be made for tooth size (Table 5). Partitioning of the diet among the species of salmon investigated is clearly a reflection of morphological differences among the species.

DISCUSSION

The calculation of unit volumes for individual prey classes is an important component of the analysis. Prey types were assumed to be in a similar state of digestion for the different size classes of each species of salmon so that calculated unit volumes would be comparable. Violation of this assumption may account for the inverse predator-prey size relationship found for sockeye and pink salmon with euphausiids and *Parathemisto*. The analysis of relative sizes of the species eaten assumes that different prey types were not more or less digested than others. This is unlikely to be strictly true, but it was assumed that differential digestability of the prey species did not significantly alter their relative sizes.

Previous work on diet description of *Oncorhynchus* species has indicated that there can be considerable variability in dietary components of a particular species. However, some general conclusions can be drawn. Sockeye salmon are the least piscivorous of the northeast Pacific *Oncorhynchus* species (Allen and Aron 1958; LeBrasseur 1966; Foerster 1968). Euphausiids have been reported consistently as a major contributor to the diet of pink salmon (Maēda 1954; Ito 1964; Takagi et al. 1981). The fish component reported has been variable, ranging from <1% to over 90% of stomach volume (Takagi et al. 1981). Chinook and coho salmon tend to be the most piscivorous (Allen and Aron 1958; Prakash 1962; Reimers 1964; LeBrasseur 1966; Machidori 1972). For chinook salmon, fish were reported to provide

TABLE 4.—Number of salmon caught with non-empty stomachs and depth of water (m) in Strait of Juan de Fuca, British Columbia. Salmon were caught by troll gear. Numbers in parentheses are percent of each species caught in each depth zone.

Depth (m)	Sockeye	Pink	Coho	Chinook
<9.1	8 (9.9)	41 (7.3)	385 (28.1)	20 (2.2)
9.1-18.3	10 (12.3)	95 (16.9)	360 (26.3)	60 (6.6)
18.3-27.4	26 (32.1)	159 (28.3)	269 (19.6)	134 (14.6)
27.4-36.6	23 (28.4)	151 (26.9)	211 (15.4)	267 (29.1)
36.6-45.7	7 (8.6)	65 (11.6)	86 (6.3)	119 (13.0)
45.7-54.8	7 (8.6)	50 (8.9)	58 (4.2)	316 (34.5)
Total	81	561	1,369	916

TABLE 5.—Comparisons of morphometric and meristic characters of Pacific salmon whose dietary components were investigated in this study.

Species	Gillraker No.[1]	Gillraker Spacing[2]	Gillraker Length[3]	Tooth size[4]
Sockeye	33.7	close	2.6	smallest
Pink	30.4	moderate	3.4	small
Coho	21.2	wide	2.1	moderate
Chinook	20.7	wide	2.0	large

[1]From Hikita (1962).
[2]From Morrow (1980).
[3]Gillraker length as percent of postorbital-hypural length. Gillraker length is from Hikita (1962), postorbital-hypural length from Beacham and Murray (1983).
[4]From Vladykov (1962), Hikita (1962).

a larger proportion of the diet of larger chinook salmon than of smaller ones (Milne 1955; Reid 1961). In my study, the fish component of the diet was similar for all size classes of chinook salmon. This may be due to differences in availability of invertebrate prey to the smaller chinook salmon among the studies. For example, Ito (1964) found that squid were the largest dietary component of chinook and coho salmon caught in drift nets in high seas fisheries. Variability in diets of the different species may be due in part to prey abundance, selection by the predator, and possible selectivity by the sampling gear used. Hook and line sampling may select fish of different diets than would perhaps gill nets. Salmon caught by trolling may have a higher component of fish in the diet than those caught by gill nets. In my study, fish did constitute a larger proportion of the diet in larger coho salmon than in smaller ones, as noted for chinook salmon. My study has examined the distribution of prey types and sizes for salmon caught from June to October only. Although the relative proportions of fish and invertebrate prey could change seasonally for the salmon species examined, the relative ranking of the species in terms of proportion of fish in their diet should remain constant.

Availability of prey types can alter markedly the proportions in a predator's diet. Herring comprised over 70% of the stomach contents of troll-caught chinook and coho salmon caught off the east and west coasts of Vancouver Island in 1957 (Prakash 1962). My study showed that during 1967-68, herring comprised <20% of the stomach contents of chinook and coho salmon in the same area. Stock abundances of herring declined rapidly in the late 1960's in British Columbia (Hourston 1978), indicating that during a period of low herring abundance, sand lance became an important dietary component of chinook and coho salmon in this area.

Pink salmon in southern British Columbia and Washington State show 2-yr cycles of abundance, with returns absent in even-numbered years. This pattern of abundance has been suggested to be a result of predation by returning adults of the dominant brood year on fry of the alternate brood year (Ricker 1962). In my study, fish other than sand lance, herring, or rockfish comprised <1% of the stomach contents of pink salmon sampled in 1967. These results suggest that predation by the dominant broodline on the alternate broodline may be neither necessary nor sufficient to account for cycles in pink salmon abundance.

The effect of prey size on selection by planktivorous fish has been examined by Werner and Hall (1974), O'Brien et al. (1976), O'Brien (1979), Gibson (1980), and Eggers (1982). Eggers found that juvenile sockeye salmon prefer large nonevasive prey, but will eat small and/or evasive prey when the former is not available. I found that as predator size increased, prey size increased also, both in terms of size of individuals within a prey type, and a shifting from smaller to larger prey types. The predators presumably decrease the amount of time and energy needed to ingest a given amount of food by switching from smaller to larger prey, given that the large prey types are sufficiently abundant. Werner and Hall (1974) attributed a preference by predators for only a part of the prey types available as a method for increasing foraging efficiency. These results suggest that the salmon species examined do select prey both for size and availability, presumably to increase foraging efficiency.

Morphological differences and diet partitioning have been previously noted for many fish species (Keast and Webb 1966; Hyatt 1979). As outlined by Hyatt (1979), many planktivorous feeding fish tend to have numerous, well-developed, close-set gillrakers. My study indicated that the more piscivorous chinook and coho salmon have fewer gillrakers than the more planktivorous sockeye and pink salmon. Lake trout, *Salvelinus namaycush*, populations that are more planktivorous also have more and longer gillrakers than less planktivorous ones (Martin and Sandercock 1967). *Oncorhynchus masou* (masou or cherry salmon), found in the western Pacific Ocean, has fewer gillrakers than either chinook or coho salmon (Hikita 1962) and, as an adult, feeds largely on fish (Tanaka 1965). Chum, *O. keta*, salmon have an average of 2-3 more gillrakers than chinook and coho (Hikita 1962), and the diet of chum salmon sampled in the spring and summer during 1956-63 in the North Pacific comprised between 10 and 35% fish (Neave et al. 1976). In the genus *Oncorhynchus*, as gillraker number declines, the proportion of fish in the diet increases. Morphological differences among the species account for a greater partitioning of the diet than do differences in water depths in which the individual species are located.

Pacific salmon are adaptable in their diet, shifting their preferred prey species in relation to prey size and abundance. It seems unlikely that salmon abundance is affected by the abundance of any one type of prey. For example, the decline in abundance of British Columbia herring stocks was not followed immediately by declines in salmon abundance. Growth rates of salmon may be affected by changes in diet and this could have an impact on stock population dynamics.

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LITERATURE CITED

ALLEN, G. H., AND W. ARON.
1958. Food of the salmonid fishes of the western North Pacific Ocean. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 237, 11 p.

BEACHAM, T. D., AND C. B. MURRAY.
1983. Sexual dimorphism in the adipose fin of Pacific salmon (*Oncorhynchus*). Can. J. Fish. Aquat. Sci. 40:2019-2024.

EGGERS, D. M.
1982. Planktivore preference by prey size. Ecology 63:381-390.

FOERSTER, R. E.
1968. The sockeye salmon, *Oncorhynchus nerka*. Bull. Fish. Res. Board Can. 162:1-422.

FRENCH, R., H. BILTON, M. OSAKO, AND A. HARTT.
1976. Distribution and origin of sockeye salmon (*Oncorhynchus nerka*) in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 34, 113 p.

GIBSON, R. M.
1980. Optimal prey-size selection by three-spine sticklebacks (*Gasterosteus aculeatus*): a test of the apparent-size hypothesis. Z. Tierpsychol. 52:291-307.

GODFREY, H., K. A. HENRY, AND S. MACHIDORI.
1975. Distribution and abundance of coho salmon in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 31, 80 p.

GRAHAM, C. C., AND A. W. ARGUE.
1972. Basic data on Pacific salmon stomach contents and effort for 1967 and 1968 test trolling catches in Juan de Fuca Strait, British Columbia. Can. Dep. Environ. Fish. Serv., MS Rep. 1972-76, 405 p.

HIKITA, T.
1962. Ecological and morphological studies of the genus *Oncorhynchus* (Salmonidae) with particular consideration on phylogeny. Sci. Rep. Hokkaido Salmon Hatchery 17, 60 p.

HOURSTON, A. S.
1978. The decline and recovery of Canada's Pacific herring stocks. Can. Fish. Mar. Serv. Tech. Rep. 784, 17 p.

HYATT, K. D.
1979. Feeding Strategy. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. VIII, Bioenergetics and growth, p. 71-119. Acad. Press, N.Y.

HYNES, H. B. N.
1950. The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) with a review of the methods used in studies of the food of fishes. J. Anim. Ecol. 19:36-58.

ITO, J.
1964. Food and feeding habits of Pacific salmon (genus *Oncorhynchus*) in their oceanic life. Hokkaido Reg. Fish. Res. Lab. Bull. 29:85-97. (Engl. transl., Fish. Res. Board Can. Transl. Ser., 1309.)

KEAST, A., AND D. WEBB.
1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Board Can. 23:1845-1874.

LAGLER, K. F., J. E. BARDACH, AND R. R. MILLER.
1962. Ichthyology. John Wiley and Sons, Inc., N.Y., 545 p.

LEBRASSEUR, R. J.
1966. Stomach contents of salmon and steelhead trout in the northeastern Pacific Ocean. J. Fish. Res. Board Can. 23: 85-100.

MACHIDORI, S.
1972. Observations on latitudinal distribution of offshore coho salmon in early summer, with reference to water temperature and food organisms. Jpn. Far Seas Fish. Res. Lab. Bull. 6, p. 101-110.

MAËDA, H.
1954. Ecological analyses of pelagic shoals—I. Analysis of salmon gill-net association in the Aleutians. (1) Quantitative analysis of food. Jpn. J. Ichthyol. 3:223-231.

MAJOR, R. L., J. ITO, S. ITO, AND H. GODFREY.
1978. Distribution and origin of chinook salmon (*Oncorhynchus tshawytscha*) in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 38, 54 p.

MARTIN, N. V., AND F. K. SANDERCOCK.
1967. Pyloric caeca and gill raker development in lake trout, *Salvelinus namaycush*, in Algonquin park, Ontario. J. Fish. Res. Board Can. 24:965-974.

MILNE, D. J.
1955. Selectivity of trolling lures. Fish. Res. Board Can. Prog. Rep. Pac. Coast Stn. 103:3-5.

MORROW, J. E.
1980. The freshwater fishes of Alaska. Alaska Northwest Publ. Co., Anchorage, AK, 248 p.

NEAVE, F., T. YONEMORI, AND R. G. BAKKALA.
1976. Distribution and origin of chum salmon in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 35, 79 p.

O'BRIEN, W. J.
1979. The predator-prey interaction of planktivorous fish and zooplankton. Am. Sci. 67:572-581.

O'BRIEN, W. J., N. A. SLADE, AND G. L. VINYARD.
1976. Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). Ecology 57:1304-1310.

PARKER, R. R.
1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. J. Fish. Res. Board Can. 28: 1503-1510.

PRAKASH, A.
1962. Seasonal changes in feeding of coho and chinook (spring) salmon in southern British Columbia waters. J. Fish. Res. Board Can. 19:851-866.

REID, G. M.
1961. Stomach content analysis of troll-caught king and coho salmon, Southeastern Alaska, 1957-58. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 379, 8 p.

REIMERS, P. E.
1964. A modified method of analyzing stomach contents with notes on the food habits of coho salmon in the coastal waters of Oregon and southern Washington. Fish. Comm. Oreg. Res. Briefs 10, p. 46-56.

RICKER, W. E.
1962. Regulation of the abundance of pink salmon populations.

In N. J. Wilimovsky (editor), Symposium on Pink Salmon, p. 155-211. Inst. Fish., Univ. Br. Columbia, Vancouver, B.C.

TAKAGI, K., K. V. ARO, A. C. HARTT, AND M. B. DELL.
1981. Distribution and origin of pink salmon (*Oncorhynchus gorbuscha*) in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 40, 195 p.

TANAKA, S.
1965. A review of the biological information on masu salmon (*Oncorhynchus masou*). Int. North Pac. Fish. Comm. Bull. 16, p. 75-135.

VLADYKOV, V. D.
1962. Osteological studies of Pacific salmon of the genus *Oncorhynchus*. Bull. Fish. Res. Board Can. 136, 172 p.

WERNER, E. E., AND D. J. HALL.
1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55:1042-1052.

DETERMINING AGE OF LARVAL FISH WITH THE OTOLITH INCREMENT TECHNIQUE

CYNTHIA JONES[1]

ABSTRACT

Aging of larval fish from otoliths rests on the assumption that increments are formed daily. Indeed, proper validation of the relationship between increment deposition and age is fundamental to accurate age determination of field-captured fish. To evaluate the universality of daily deposition of otolith increments, the literature was reviewed and exceptions discussed.

Laboratory studies under optimal conditions generally (17 species out of 20) show that larvae deposit daily increments. However, in studies that examined increment deposition under suboptimal or extreme conditions, deposition was not daily in over half of the species. Nondaily deposition caused by extreme conditions (e.g., total starvation, abnormal photoperiod) may not invalidate the otolith increment technique if those conditions do not occur in the field. Nondaily deposition under suboptimal conditions (e.g., low temperature, intermittent starvation) that larvae may face in nature cause concern about this technique for aging field-captured larvae. Deposition in many species has not been examined under suboptimal conditions, nor has the effect of suboptimal conditions been shown on the age at first increment formation. The literature shows that the technique should be validated under both optimal conditions and those that mimic nature.

Otoliths have been used to age fish since Reibisch (1899) first observed annular ring formation in *Pleuronectes platessa* (as reported in Ricker 1975). Assessing age by counting annular rings works well in adults of temperate species where pronounced seasonal changes in growth result in bands (formed from tightly spaced growth increments deposited in the winter) in the otolith which correspond to each year of life. Discovery of fine increments, analogous to annual rings, but instead formed daily, has permitted the age of larval fish to be determined.

While studying temperate water species, Pannella (1971) observed that about 360 fine increments occurred between annular rings and suggested that these were deposited daily. He used this knowledge when reading the otoliths of adult tropical fish (whose otoliths also had fine increments) to show patterns of growth that were grouped into 14- and 28-d cycles (Pannella 1974).

The initial application of the otolith aging technique to larval fish was done by Brothers et al. (1976). Daily increment deposition was verified for northern anchovy, *Engraulus mordax*, and California grunion, *Leuresthes tenuis*, which were reared from eggs in the laboratory. Since this initial application, the otolith increment technique has been used widely to estimate age in at least 29 species of larval fish. It has been used in freshwater and marine species, and applied to field-captured species, at times without adequate validation.

The ultimate purpose in developing the otolith aging technique for application to young fish is the ability to accurately age field larvae and juveniles. If the technique is to be applied directly to the field, based on conclusions drawn from rearing larvae in the laboratory, then the deposition of increments must be daily under conditions experienced in the field during these early life stages. The applicability of this technique relies on the assumption that 1) either surviving larvae (or sampled larvae) are those that grew under moderately good conditions (few larvae under suboptimal conditions survive) or 2) larvae can encounter suboptimal conditions, a proportion of these larvae will survive, and increment deposition is not affected by these suboptimal conditions. The first assumption is difficult to evaluate without using the hypothesis that increments are daily. The second assumption has been tested and the results can be summarized. The second assumption is based on increment deposition being triggered by a zeitgeber, an external factor that entrains a diel cycle within the larvae.

Validation of daily increment deposition under conditions within the natural range of experience of the larvae is fundamental to accurate estimation of age in field-captured fish. When the estimation technique

[1]Graduate School of Oceanography, University of Rhode Island, Kingston, RI 01882-1197; present address: Department of Natural Resources, Cornell University, Ithaca, NY 14853.

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used to age larvae is inaccurate, estimates of growth and mortality, which rely on knowledge of age, will also be inaccurate.

The purpose of this paper is to discuss the use of the otolith increment technique to age larval fish. The published literature is used to evaluate the hypothesis, H_0: Larval age is equal to otolith increment count (plus age at first increment deposition) under conditions that are encountered in the field. An additional idea can be evaluated: That time of initial increment deposition is influenced by incubation time.

The paper will discuss the factors which affect deposition of increments, validation studies that have been performed, and application of the technique in the field. Factors which are likely to affect increment deposition in the field must be assessed by the validation procedure. In addition, the adequacy of validation that has been performed is evaluated, and ramifications in field applications are discussed.

FACTORS AFFECTING DEPOSITION RATES

Mechanisms that have been postulated as initiators of differentiation of otolith microstructure are photoperiod, feeding, and temperature. Increment deposition has been tested in the literature under two conditions: 1) tests within the natural range of experience of the fish which could be optimal (nonstressful) and suboptimal (stressful), and 2) abnormal conditions that are wholly outside of their experience.

Taubert and Coble (1977) stated that photoperiod entrained a diel clock that resulted in daily formation of otolith increments. Tanaka et al. (1981) studied the formation of increments in *Tilapia nilotica* using scanning electron microscopy and found that the fast growth (incremental) zone started a few hours after light stimulus and that the slow growth (discontinuous) zone was formed immediately after light stimulus. Neither change in photoperiod length nor feeding time affected increment initiation. Brothers and McFarland (1981), however, reported that the discontinuous zone began near midnight. These results are contradictory, and without further investigations force the conclusion that the temporal formation of increments is species-specific.

Abnormal photoperiods have been shown to disrupt daily increment formation in *Fundulus heteroclitus* (Radtke and Dean 1982) and in *Tilapia mossambica* (Taubert and Coble 1977). Constant light, however, did not disrupt daily increment formation in *Oncorhynchus tshawytscha* (Neilson and Geen 1982) or in *Scophthalmus maximus* (Geffen 1982).

Unlike photoperiod changes, which are regular and gradual in nature, feeding times can occur at irregular intervals and might cause deviations in daily increment deposition. Two studies have tested the effects of feeding within the normal range experienced by fish larvae. Neilson and Geen (1982) found that subdaily increments could be induced through frequent discrete feedings: feeding four times a day resulted in formation of more than one increment in *Oncorhynchus tshawytscha*. Daily and subdaily increments were not distinguished in counts. Tanaka et al. (1981) found conversely that feeding time had no effect on the initiation of increment formation in *Tilapia nilotica*. Larvae were fed once a day, but the times of feeding were changed. Perhaps multiple feeding during the day results in the subdaily increments that sometimes appear in otoliths. The effect of starvation (an extreme circumstance in the field) on increment deposition has been tested in only three species: *Scophthalmus maximus* (Geffen 1982), *Morone saxatilis* (Jones 1984), and *Oncorhynchus nerka* (Marshall and Parker 1982). Geffen raised the turbot larvae on rotifers and *Artemia* until they were 10 d old. Larvae were then starved for 23 d. Jones did not supply exogenous food from hatch onward. Both Geffen and Jones found that starvation disrupted increment formation. Marshall and Parker fed their sockeye salmon larvae for the first 3 wk of life, and then starved them for 2 wk. Marshall and Parker found that starvation over 2 wk had no effect on increment deposition. It is possible that the difference might reflect different age-specific sensitivity to starvation, rather than species-specific responses.

Brothers (1978) has linked temperature as a prime factor in increment deposition. Working with temperate stream populations, he has found that diel temperature changes result in daily increment formation. Brothers (1978) stated that "six or more increments per day may be formed as the result of short term, . . . relatively minor. . . temperature fluctuations." Other investigators (Radtke and Dean 1982; Geffen 1982) found that small temperature changes had no effect on the rate of increment deposition. Apparently, temperature response is also species-specific.

LABORATORY STUDIES OF INCREMENT DEPOSITION

Initial Ring Deposition

When fish are raised in the laboratory from eggs

through the larval stages, two parameters fundamental to application of the increment technique to field populations can be determined: 1) age at first increment deposition and 2) testing of daily increment deposition under artificial conditions. Age at initial increment deposition for 18 species of fish is listed in Table 1. Radtke (1978) speculated that in species having slowly developing embryos, initial deposition occurs at, or before, hatch; in species having rapidly developing embryos, initial increment deposition does not occur until yolk-sac absorption or first feeding. This hypothesis is not substantiated in the currently published literature. Information for nine species of laboratory-reared fish larvae (Table 2) shows no such trend for data currently reported in the literature. Even for the same suborder, Clupeoidei, opposite development and initial increment deposition patterns exist for herring (*Clupea harengus*) and the northern anchovy.

The Case for Daily Increment Deposition

Seventeen species have shown consistent daily deposition of increments under what are presumed to be good conditions for growth. The species that have shown daily increment deposition come from both freshwater and marine habitats and encompass a wide variety of lifestyles. In addition, six species held in the laboratory and sampled over known periods of time demonstrated daily increment deposition (Table 3). Four investigation groups (Struhsaker and Uchiyama 1976 for *Stolephorus purpureus*, Taubert and Coble 1977 for *Lepomis macrochirus*, Campana and Neilson 1982, Wilson and Larkin 1980 for *Oncorhynchus nerka*) brought larvae and juveniles into the laboratory, reared them for a period of time, then correlated increment counts to days of captivity. Schmidt and Fabrizio (1980) took consecutive samples from a field population of *Micropterus salmoides*, which had a short spawning period and correlated the time between samples to the change in mean increment count.

Lack of Daily Deposition Rates

The most controversial results obtained so far come from studies of increment deposition in larval *Clupea harengus* (Table 1). Agreement for daily increment deposition has not been obtained. Studies that observed daily deposition by Gjøsaeter[2] and and Gjøsaeter and Øiestad (1981) indicate that increments are deposited with roughly daily periodicity and that initial increment deposition begins at first feeding (4-5 d). Gjøsaeter and Øiestad (1981) found that 99 increments were formed in 97-d-old larvae. Gjøsaeter, however, cautioned that these results were based on small sample sizes. Lough et al. (1982) reported on larval herring reared in the laboratory that lived until age 18 d. They did confirm that increment deposition began at yolk-sac absorption, but did not find that the increments were daily. In fact, only three increments were laid down within 18 d. Lack of confirmation of daily deposition is easy to dismiss, since the larvae did not survive past 18 d.

However, Geffen (1982) has demonstrated an interaction between growth rate and increment deposition rate. Only under circumstances of very fast growth, 0.42 mm/d (a rate which is faster than growth rates postulated for field animals) did increment deposition approach daily periodicity (0.92 increments/d). It is noteworthy that the growth rates in her study were related to container size; faster growth occurs in bigger containers. The variance of increment count at age is small and homogeneous only under the fastest growth condition (Norway Pond). The increasing variance with age in the other conditions leads to the speculation that some of these larvae were unknowingly starving. However, since the slope of the regression line for the Norway Pond condition is significantly different than 1 increment/d, this result cannot be dismissed. There would be obvious value in repeating these experiments. Geffen also found that increment formation did not begin before yolk-sac absorption and was in agreement with the other investigators on this point. The literature (Table 1) shows only one case (*Oncorhynchus nerka*) where independent investigators have confirmed daily increment deposition (Wilson and Larkin 1980; Marshall and Parker 1982).

Geffen (1982) found that increment deposition was also a function of growth in *Scophthalmus maximus* (Table 4) under various conditions of temperature and photoperiod. Under two conditions—1) 20°C, constant light, and 2) 24°C, 12L:12D—increments were deposited daily. For all other conditions increments were not daily. Under all conditions, deposition rate was a function of length. Although Geffen did not point this out, comparisons of growth at different temperatures can also be drawn from the data. Larvae were grown under 20°C and 24°C, both under a 12L:12D cycle. Larvae grew faster and deposited more increments at 24°C. Such differences in temperature might be used to explain differences in increment deposition except that the other case

[2]Harold Gjøsaeter, Institute of Marine Research, P.O. Box 1870 - 5011 Bergen, Norway, pers. commun. February 1983.

TABLE 1.—Otolith increment deposition for laboratory reared larval fish of known age. ff =

Species	Source	Are increments daily?	Time of increment initiation	Validation	N	
Clupea harengus	Gjøsaeter and Øiestad (1981)	yes	after ff	correspondence between age and rings Rings = 99, Age = 97 d	10	eg
	Gjøsaeter (1981)	yes	4-5 d old or ff	slope = 0.95 rings/d	31	6-
	Geffen (1982)	no	1st rings at ysa	ring deposition depends on growth rate	227	eg
	Lough et al. (1982)	no	1st ring 4.5 d	1st 3 rings in 18 d	57	eg
Engraulis mordax	Brothers et al. (1976)	yes	after ysa	correspondence between age and rings (interaction growth and rings)	88	6-
Fundulus heteroclitus	Radtke (1978); Radtke and Dean (1982)	yes	from before hatch	slope = 1 ring/d	280 (temp) 270 (photoperiod)	eg
Gadus morhua	Radtke and Waiwood (1980)	yes	day after hatch	correspondence between age and rings	≅40	eg
Lepomis cyanellus	Taubert and Coble (1977)	yes	after swim up	correspondence between age and rings independent of growth	54	eg
Leurestes tenuis	Brothers et al. (1976)	yes	at hatching	correspondence between age and rings	15	eg
Menidia menidia	Barkman (1978)	yes		slope = 0.97 rings/d independent of growth	55	eg
Morone saxatilis	Jones (1984)	sometimes	at ysa	regression analysis	148	eg
Mugil cephalus	Radtke (1984)	yes	1 day after hatch	regression and correspondence	50	eg
Oncorhynchus keta	Volk et al. (1984)	yes	at hatch	regression analysis	32(?)	ha

ff = first feeding, ysa = yolk-sac absorption, ns = not stated.

	Life history Stage	Rearing conditions				
		Light	Temp	Feeding	Salinity	Other
	eggs-100 d	natural	ns	plankton	ns	
	6-135 d	ns	ns	ns	ns	
	eggs-100 d	18L/6D	8°-14°C	variety	seawater	various container sizes
	eggs-18 d	ns	10°C	plankton	ns	
	6-94 d	14L/10D	ns	ns	ns	
p) to- od)	eggs-30 d	several regimes	24°C 30°C	*Artemia*	30‰	
	eggs-30 d	natural	4°C	plankton	18-25‰	2 tank sizes
	eggs-170 d	15L/9D	24°-27°C	plankton and *Artemia*		
	eggs-26 d	natural	17°-20°C	*Artemia*	ns	
	eggs-68 d	12L/12D	19.4°-21.6°C	*Artemia*	31‰	
	eggs-97 d	14L/10D	18°C	*Artemia*	0-10‰	4 L jars
	eggs-52 d	ambient	24.0° ± 0.9°C	Rotifers, fish chow	32.0 ± 0.4‰	500 L tanks (flow through)
	hatch-190 d	ambient	7.6°-10.2°C	Copepods and pellets	29.8-33.6‰	10 L tanks

TABLE 1.—*Continued.*

Species	Source	Are increments daily?	Time of increment initiation	Validation
Oncorhynchus nerka	Marshall and Parker (1982)	yes	at hatch but can be interrupted	correspondence between age and ring
Oncorhynchus tshawytscha	Neilson and Geen (1982)	sometimes	1 or more/d	regression and correspondence between age and rings
Pagrus major	Tsuji and Aoyama (1982)	yes	from hatching	slope = ring/d independent of growth
Parophrys vetulus	Laroche et al. (1982)	yes	4-5 d old	correspondence between age and ring
Pseudopleuronectes americanus	Radtke and Scherer (1982)	yes	after ysa	regression and correspondence between age and rings
Salmo salar	Geffen (1983)	no	depends on physiology	regressions and ANC
Sebastes spp.	Radtke (1980)	yes	from birth	correspondence between age and ring Lab data not present
Scophthalmus maximus	Geffen (1982)	no	depends on growth	regressions
	Rosenberg and Haugen (1982)	yes	at hatch	back-calculated hatch date
Tilapia mossambica	Taubert and Coble (1977)	yes	when they leave mouth	data not presented
Tilapia nilotica	Tanaka et al. (1981)	yes	at hatch	correspondence between age and ring

on	*N*	Life history Stage	Rearing conditions				
			Light	Temp	Feeding	Salinity	Other
ce be- nd rings	≅440	eggs-93 d	natural	ambient >10°C <10°C	fed 3 wk fed versus starved	ns	200 L tanks
d corre- between gs	34 (feed- ing) 10 (temp) ≅12 (photo- period)	fry-90 d	12L/12D 24D 24L	4°-12°C	excess 1x/d 4x/d	ns	28 L tanks
l t of	not given	eggs-30 d	24L 12L/12D	20°C	2x/d variety of food	ns	1,000 L tanks
ce be- nd rings	136	eggs-26 d	14L/10D	12°-13°C	variety	seawater	4 and 8-9 L tanks
d corre- between gs	≅200	eggs-34 d	12L/12D	5°-8°C	variety	ns	10 L tank
nd ANOVA	36 (temp) 56 (light and temp)	embryos	24D 12L/12D 6L/6D	8°, 10°, and 15°C	*Artemia*	not appli- cable	15 cm dishes
ce be- nd rings presented	not given	not given eggs - ?	12L/12D	ns	ns		
	72	eggs-23 d	24L 6L/6D 12L/12D	20°C 24°C	rotifers and *Artemia*	seawater	30 L tank
d hatch	62	2-12 d	ambient	18.5°- 22.5°C	fed and starved	ns	2,000 m^3 tank
nted	≅300	eggs-60 d	15L/9D	24°-27°C	trout food	ns	
ce be- nd rings	20 (rings) 80 (feed- ing)	eggs-28 d	12L/12D 18L/6D 6L/18D	27.5°C	ns	ns	60 L tank

TABLE 2.—Relationship between incubation time, egg size, and initial increment deposition: Determing whether species with long incubation and large eggs initiate increment deposition on or before hatch, while species with short incubation and small eggs initiate increments at first feeding or yolk sac absorption. ysa = yolk sac absorption.

Species	Temperature	Source	Incubation time	Source	Initial increment deposition	Source	Egg size (mm)	Source
Clupea harengus	≅10°C	Blaxter (1969)	≅18 d	Blaxter (1969)	4-5 d ysa	See Table 1	0.9-1.7	Blaxter (1969)
Engraulis mordax	11°-21°C	Lasker (1964)	1-5d	Lasker (1964)	≅5 d	Brothers et al. (1976)	≅2	
Fundulus heteroclitus	24°-30°C	Radtke (1978)	14 d	Radtke (1978)	Before hatch	Radtke (1978)	2	Armstrong and Child (1965)
Gadus morhua	4°C	Radtke and Waiwood (1980)	19 d	Radtke and Waiwood (1980)	1 d	Radtke and Waiwood (1980)	1.1-1.6	Blaxter (1969)
Menidia menidia	19.4°-21.6°C	Barkman (1978)	7-10 d at 23°-25°C	Barkmann and Beck (1976)	Before hatch from regression	Barkman (1978)	1.2	Barkmann and Beck (1978)
Morone saxatilis	18°C	Jones (1984)	2 d	Jones (1984)	6-9 d	Jones (1984)		
Parophrys vetulus	20°C	Laroche et al. (1982)	3-3½ d	Laroche et al. (1982)	4-5 d	Laroche et al. (1982)		
Pseudopleuronectes americanus	5°-8°C	Radtke and Scherer (1982)	14 d at 8°C	McPhee[1]	9-10 d	Radtke and Scherer (1982)	0.8	Smigielski and Arnold (1972)
Tilapia nilotica	27°C	Tanaka et al. (1981)	4 d	Tanaka et al. (1981)	At hatch	Tanaka et al. (1981)		

[1]Grace McPhee, P.O. Box 210972, Auke Bay, AK 99821, per. commun. summer 1983.

TABLE 3.—Otolith increment deposition for larval fish maintained in the laboratory over a known time span.

Species	Source	Known-age span	Are increments daily?	Validation	Number of fish
Lepomis gibbosus	Taubert and Coble (1977)	≅6-176 d	yes after swim up	Correspondence between age and rings	
Lepomis macrochirus	Taubert and Coble (1977)	≅6-125 d	yes after swim up	Correspondence between age and rings	
Micropterus salmoides	Schmidt and Fabrizio (1980)	Between 47 and 81 rings	yes	Correlation between change in ring count and time interval	98
Oncorhynchus nerka	Wilson and Larkin (1980)	Between 14 and 26 rings	yes	Slope = 1 ring/d	100
Platichthys stellatus	Campana and Neilson (1982)	8-10 mo old	yes	Slope = 1 ring/d	13 (in situ) 81 (temp and light)
Stolephorus purpureus	Struhsaker and Uchiyama (1976)		yes	Correspondence between rings and days	174

of daily deposition (24L, 20°C) would be an anomaly under this hypothesis.

Ten studies have investigated deposition rates under suboptimal, extreme or varying conditions (Table 4). These studies are important to the understanding of the underlying mechanisms causing increment deposition. Two studies, one by Radtke and Dean (1982) and one by Taubert and Coble (1977), demonstrated disruption of daily increment formation under extreme or abnormal changes in photoperiod. Taubert and Coble (1977) found that in simulated winter conditions, cold temperature and shorter photoperiod resulted in cessation of increment formation in *Lepomis cyanellus*. At and below temperatures of 10°C, growth and increment deposition ceased. If such changes occurred gradually, as occurs in the normal lifetime of fish, acclimation to these temperature changes might be expected through most of the temperature range. Within normal physiological limits (especially where some growth continued), increment deposition would be assumed to continue regularly. However, Marshall and Parker (1982) also found that temperatures below 10°C resulted in cessation of increment deposition in sockeye salmon. Hence two studies have shown that increment deposition is not maintained

TABLE 4.—Otolith increment deposition for known-age larval fish under experiments where various culture conditions were tested.

Species	Source	Conditions of growth				Effect on increment deposition
		Light	Food	Temp	Other	
Clupea harengus	Geffen (1982)				tank size 120 L, 500 L, 310 m^3 4,440 m^3	Increment deposition rate was related to growth rate. Also, larvae grew faster in bigger container and deposited more rings.
Fundulus heteroclitus	Radtke and Dean (1982)	Multiple L/D conditions		24°C 30°C		Temperature affects growth rate, but not increment deposition. Increment deposition rate disrupted under constant dark or under <24-h photoperiod.
Lepomis cyanellus	Taubert and Coble (1977)	15L/9D 10L/14D		4°-25°C		Fewer hours of light and lower temperature resulted in cessation of ring deposition. At 10°C or less, growth ceased, as did increment formation.
Morone saxatilis	Jones (1984)	14L/10D	Fed, starved, intermittent starved, then fed	18°C		Increment deposition rate was disrupted during periods of starvation. Increments not daily in sagittae during 2-3 mo under optimal conditions.
Oncorhynchus nerka	Marshall and Parker (1982)		Fed Starved	<10°C >10°C		Starvation for 10 d did not affect increment deposition. Temperatures <10°C resulted in cessation of increment formation.
Oncorhynchus tshawytscha	Neilson and Geen (1982)	24D 24L 12L/12D	4×/d 1×/d	11°C 5.2°C		Formation of increments was related to feeding frequency. Temperature affected width of increment, not deposition rate. Photoperiod had no effect.
Salmo salar	Geffen (1983)	24D 6L/6D 12L/12D		8°C 10°C 15°C		Rate of ring deposition increased with increased light and temperature.
Scophthalmus maximus	Geffen (1982)	24L 6L/6D 12L/12D	Fed Starved	20°C 24°C		Daily increments formed under 24L-20°C and 12L/12D-24°C. Starvation and 6L/6D interrupted increment formation. Increment formation related to growth rate.
Tilapia mossambica	Taubert and Coble (1977)	24L 24L/12D 15L/9D	Every 3 h Every 6 h Intermittent			Daily increments formed under 24-h photoperiod, not under 36-h cycle nor constant light. Subdaily increments induced. No effect from feeding cycle.
Tilapia nilotica	Tanaka et al. (1981)	12L/12D 18L/6D 6L/18D	3 h before dark 3 h after light			Formation of increment triggered by light stimulus. Feeding time had no effect under 12L/12D.

below certain temperatures. In two other studies where temperatures ranged from 24°C to 30°C (Radtke and Dean 1982) and from 5.2°C to 11°C (Neilson and Geen 1982), these temperatures affected the growth rate and width of increments, but did not alter the increment deposition rate.

Six studies looked at the relationship between feeding and daily increment deposition. Jones (1984), Geffen (1982), and Marshall and Parker (1982) showed opposite effects of starvation on increment deposition. Jones (1984) found that starvation of young larvae for 2 wk resulted in deposition of only one increment every other day. However, in addition to lengthy starvation, the effect of short-term, intermittent periods of starvation was also studied and resulted in nondaily increment formation. Geffen (1982) found that starvation interrupted deposition in larval turbot, while Marshall and Parker (1982) found that starvation for 2 wk had no effect on daily deposition in sockeye salmon. Long-term starvation experiments test for interruption of increment deposition under extreme conditions. To age larvae in the field, it is important to determine the minimum number of consecutive days of starvation needed to affect increment deposition. Once these values are known, it is important to determine whether field larvae actually experience these levels of deprivation.

Three studies looked at feeding time or frequency on increment deposition. Neilson and Geen (1982) found that feeding frequency could induce forma-

tion of subdaily increments in *Oncorhynchus tshawytscha*. Both Tanaka et al. (1981) and Taubert and Coble (1977) found that feeding time had no effect on increment deposition in larval mouthbrooders (*Tilapia nilotica* and *T. mossambica*).

Little agreement has been reached in these studies concerning the effect of light, temperature, or feeding on increment formation. The effects of variability in temperature, food, salinity, and other factors (extreme photoperiods would not be encountered) relate directly to the problems of accurately aging larvae from the field. At the moment, environmental effects appear to be species-specific. Indeed, specific tests of the effect of suboptimal conditions (which are likely to occur in the field) on increment deposition have rarely appeared in the literature. Such analyses, conducted for more species, might confirm the conventional wisdom that deviation from daily deposition rate is abnormal. However, the questions raised by the studies reviewed here (Table 4) remain to be fully addressed or dispelled.

APPLICATION IN THE FIELD

Current Applications

The ability to age larval fish precisely provides more accurate estimates of growth, mortality, and the ability to discern the effects of environmental variables on the first year of life. Rapid growth in the first months of life has commonly been thought to be critical to survival. Evidence in support of this hypothesis (Brothers et al. 1983) and contrary to it (Methot 1983) exists.

The otolith increment aging technique has been

TABLE 5.—Application of the otolith increment aging technique in field grown larvae.

Species	Source	Based on prior validations (validations in Table 1)	Validation source	Sample size	Application
Ammodytes dubious	Scott (1973)	no		71	Back-calculated growth.
Clupea harengus	Graham and Joule (1981)	controversial Geffen (1982) found deposition depended on growth rate. Gjøsaeter and Øiestad (1981) found deposition was daily. See Table 1 for details.	See Table 1 for details	545	Determine hatching dates and delineate cohorts which are followed through time.
	Townsend and Graham (1981)			300	Determine hatching dates and assess growth rates of larval cohorts. Noted cessation of growth in winter.
	Lough et al. (1982)			311	Use age to delineate growth. Fit Gompertz function of length-at-age data.
	Jones (1985)			481	Determination of within-season growth differences based on uncertainty in otolith aging.
Engraulis mordax	Methot and Kramer (1979)	yes	Brothers et al. (1976)	587	Fit Gompertz function to length-at-age data to obtain growth rates. Also mention that starvation slowed increment deposition.
Fundulus heteroclitus	Radtke and Dean (1982)	yes	Radtke and Dean (1982)	not given	Compare length-frequency histograms with increment-frequency histograms. Show relationship between hatching and lunar cycle.
Gadus morhua	Gjøsaeter and Tilseth (1981)	yes	Radtke and Waiwood (1980)	30	Regression of age estimated from morphologic development versus increment counts.
	Steffenson (1980)	yes	Radtke and Waiwood (1980)	138	Back-calculated hatch date from increments. Compare these to field observations of spawning time.
Haemulon flavolineatum	Brothers and McFarland (1981)	no, but refers to data as otolith age		≅306	Correspondence between otolith microstructure and events in the life history. Derive "otolith" growth rates.
Halichoeres bivittatus	Victor (1982)	yes	marked juveniles	10	Determine daily deposition of increments and use to determine settling pattern.
Lepomis macrochirus	Taubert and Coble (1977)	yes	Taubert and Coble (1977)	≅150	Allometric relationship between otolith length and fish length tested for 2 lakes.

applied to larval field populations of many species of fish (Table 5). Most applications have been based on laboratory validation of daily increment deposition for the individual species studied. Some have not. Methot and Kramer (1979), based on validation of daily increment deposition by Brothers et al. (1976), obtained growth rates for wild populations of *Engraulis mordax* by fitting a Gompertz function to length-at-age data. Various other field applications of the increment aging technique are listed in Table 5. Of special interest is a comparison of growth estimates for *Parophrys vetulus* from modal progression of length frequencies and otolith increments (Laroche et al. 1982). Growth based on the increment count method was 2-3 times faster. If the increment count method proves to be accurate, then mortality estimates could be considerably changed.

For at least four species listed in Table 5, laboratory validation was not conducted. These applications assume a given age at initial deposition and daily increment deposition thereafter. The validity of these assumptions depends on the species and on the sensitivity of the application to inexactness in the age estimation. For example, controversial results have been obtained for larval herring, *Clupea harengus*. Geffen (1982) showed that growth rates could be overestimated by as much as three times the actual rate. However, analysis of Gulf of Maine herring data (Jones 1985) showed that differences in growth between larvae hatched early and late in the season could be drawn. Until sensitivity analyses, laboratory verification, or other evidence exists to assure daily increment formation as a universal phenomenon under suboptimal conditions, there will be some doubt about the accuracy of aging field-captured larvae.

Transition from the Laboratory to the Field

A question that remains to be answered when applying laboratory-derived increment deposition

TABLE 5.—*Continued.*

Species	Source	Based on prior validations (validations in Table 1)	Validation source	Sample size	Application
Menidia menidia	Barkman et al. (1981)	yes	Barkman (1978)	105 (lab)	Compare growth in lab and field. Calculate hatching dates. Compare growth between early and late hatched larvae.
Morone saxatilis	Brothers et al. (1976)	no		5	Correspondence between increment estimated age and spawning season. Growth through lifetime of juvenile.
Oncorhynchus nerka	Wilson and Larkin (1982)	yes	Wilson and Larkin (1980)	64	Relationship between fish weight and otolith size. Use daily increments as time marker.
Parophrys vetulus	Laroche et al. (1982)	yes	Laroche et al. (1982)	331	Determine growth of aged field larvae and fit Gompertz and von Bertalanffy functions. Compare length-frequency and otolith techniques.
	Rosenberg and Laroche (1982)	yes	Laroche et al. (1982)	233	Growth during metamorphosis. Relate to age and transformation in morphology.
Pseudopleuronectes americanus	Radtke and Scherer (1982)	yes	Radtke and Scherer (1982)	120	Comparison of length-frequency and increment-frequency histograms for field larvae. Daily growth rate calculated. Compare growth rates over time.
Stolephorus purpureus	Struhsaker and Uchiyama (1976)	yes	Struhsaker and Uchiyama (1976)	213	Built growth curves based on age. Discussion of relationship to feeding. Preliminary study of growth rate difference between areas.
Thalassoma bifasciatum	Victor (1982) Victor (1983)	yes	Victor (1982) marked juveniles	68 103	Determine daily increment deposition. Calculate pattern of settlement based on age estimate.
28 species of coral reef fish	Brothers et al. (1983)	no		210	Determine length of larval life prior to recruitment. Examine otoliths for marker between postlarvae to juvenile.

rates to field populations is the constancy of deposition rates between these environments. Most laboratory studies have occurred under constant temperature and salinity and under conditions of artificial food types and densities and low light intensities compared with the field. Often, increments from otoliths of laboratory-grown larvae are much fainter than those from otoliths of field-captured larvae. Since field conditions can fluctuate to extents that have been shown to cause increment disruption in laboratory situations, a way to verify daily deposition in the field would be an important contribution. A transitional step between the laboratory and the field has been made by Laurence et al. (1979) and Øiestad (1982). Laurence et al. (1979) raised known-age larvae in a flow through enclosure. This study was designed to measure the growth and survival of fish larvae exposed to varying prey concentrations in the field. Modifications of this system could be used to study increment deposition in known-age larvae exposed to field conditions. Øiestad (1982) presented a review of larval fish studies performed in enclosures. Gjøsaeter and Øiestad (1981) reared known-age larvae in large enclosures and determined increment deposition rates (Table 1). Few investigators have used such enclosures for validation of otolith increment deposition rates for field simulated studies. Enclosures should prove particularly valuable for validation and simulation of suboptimal field conditions on growth and increment deposition.

Statistical Applications

Once the veracity of daily increment deposition is established, a wide variety of statistical methods can be used in otolith studies. Statistical methods that have been employed in larval otolith studies have been linear regressions to establish increment deposition rates and curve fitting techniques to establish growth rates from length-at-age data. Linear regression has also been applied regardless of whether it actually fits the data. It is important to check for lack of fit, selection of the appropriate model, and weighting before applying linear regression blindly. It is recommended that, when possible, confidence intervals and standard deviations be included in the data presentation.

Investigators are beginning to relate increment widths, as indicators of growth, with environmental conditions (Methot and Kramer 1979; Lough et al. 1982). When increment widths are correlated directly with environmental factors, either no correlations are seen (Neilson and Geen 1982) or correlations may be spurious. Problems exist in measuring the physical conditions to which the larvae have been exposed, especially since larvae may move from one area to another. In addition, there are questions concerning food availability and its concentration and patchiness. Another consideration in relating growth to environmental conditions is that, as the fish grows, the width of the outer increments decreases proportionately to decreases in length. Better results might be obtained either with covariance analysis or by fitting a growth function to data then using the residuals in correlation tests. Investigations of residuals with exploratory techniques such as principal component analysis or canonical correlation might prove fertile.

Comparison of Scanning Electron and Light Microscopy

Scanning electron microscopy (SEM) has been used to confirm otolith structure (Dunkelberger et al. 1980; Watabe et al. 1982) and to compare increment counts with those obtained by transmitted light microscopy (Radtke and Waiwood 1980; Campana and Neilson 1982; Neilson and Geen 1982; Radtke and Dean 1982; Tsuji and Aoyama 1982; Ralston and Miyamoto 1983). Under optimal conditions, counts using both methods were equivalent except for larval cod. Radtke and Waiwood (1980), using SEM, determined that cod produced daily increments from hatch onward, while Gjøsaeter (1981), using a light microscope, did not observe increment formation until 4-5 d after hatch.

Most investigators did not verify deposition seen with the light transmission microscope with SEM studies. Confirmation with SEM is highly desirable when increments are nondaily. However, extensive use of the technique for field surveys is prohibited by the additional cost and preparation time when compared with light microscopy. In cases where suboptimal or abnormal field conditions may result in nondaily increment formation (Jones 1984), SEM, used in conjunction with ancillary techniques, may assist identification of the proportion of larvae for which age is underestimated with light microscopy.

CONCLUSIONS

The report of the otolith workshop held in Bergen, Norway (Anonymous 1982) stated that the appearance of increments in otoliths of larval fish living in diverse habitats and representing many families, argues strongly for the universality of this phenomenon. Validation that these increments are, indeed,

deposited daily has been reported in 17 out of 20 species (Table 1) grown under optimal laboratory conditions. However, evidence exists that daily deposition can be interrupted under suboptimal and abnormal conditions, or can be dependent on growth rate (Table 6). When the effect of photoperiod is ignored (changes in photoperiod are very gradual in the field), more than 50% of the tests under suboptimal and extreme conditions have shown nondaily increment deposition rates. For other species, tests under suboptimal conditions were not conducted and the effect of these conditions on increment deposition rate is undetermined. The effect of varying conditions on the age at initial increment deposition has also not been addressed. To apply the otolith aging technique to fish from the natural environment, the scientist must either assume that larvae sampled grew under optimal conditions (those exposed to suboptimal conditions died) or verify that the species almost always deposit daily increments under field encountered conditions, or establish the error bounds for the relationship between age and increment count.

Attempts to clarify the natural phenomena that drive daily increment formation have given conflicting results. Photoperiod, feeding periodicity, and temperature fluctuations have all been cited as causing daily increment formation. When these factors are within normal ranges, it is likely, for most larvae, that deposition is daily. However, for larvae experiencing conditions outside tolerable ranges or abnormal conditions, the period of formation is likely to deviate from daily deposition. It is important to determine whether the minimum exposure to suboptimal conditions which result in nondaily deposition is actually experienced by larvae in the field. These hypotheses are amenable to further testing. More basic research on the causation of increment deposition or more extensive testing under a variety of conditions for a given species will yield more information. In situ testing with known-age larvae in enclosures which closely mimic field conditions could yield valuable results. The Bergen otolith workshop report (Anonymous 1982) has recommended that increment deposition be verified for each new species, under a variety of test conditions.

Two issues, cost effectiveness and accuracy, are important in determining whether the otolith increment technique is preferable to length-frequency analysis. Recommendations made in the report from the Bergen otolith workshop (Anonymous 1982) are that "the precision of an age determination . . . be tested against other available methods . . . by a cost benefit analysis (i.e. is enough precision gained by using this method to pay the costs and effort in preparation)". A good example would be the results shown in Laroche et al. (1982) when the otolith method was compared with modal progression of length frequencies, estimated growth rates differed by a factor of 2-3. Benefits should also include nonmonetary considerations, such as decrease in error which will propagate through estimates based on age determinations (i.e., growth and mortality). Sensitivity analyses can be used to show situations where more accurate estimates are necessary.

TABLE 6.—Incidence of nondaily increment deposition for species reared under suboptimal and extreme conditions. Stars (★) indicate nondaily deposition caused by exposure to suboptimal conditions; triangles (△) indicate nondaily deposition caused by exposure to extreme conditions; circles (○) indicates no interruption of daily deposition.

Species	Light	Food	Temp	Tank size
Clupea harengus				★
Fundulus heteroclitus	★,△		○	
Lepomis cyanellus	★		★	
Morone saxatilis		★,△		
Oncorhynchus nerka		○	★	
O. tshawytscha	○	○	○	
Salmo salar	△		★	
Scophthalmus maximus	○,△	△		
Tilapia mossambica	△	○		
T. nilotica	★	○		

Specific recommendations for improving reliability and replicability are discussed in the Bergen otolith workshop report (Anonymous 1982). In addition to these, Brothers[3] has suggested that other otoliths, such as the lapillus, be used in analysis.

Aging by the otolith increment technique is a powerful tool. Not only can population estimates of growth and mortality be refined, but growth of individuals can be obtained. Issues such as the importance of environmental factors to survival, the proportion of fast growing larvae to recruitment, and demonstration of compensation in field larvae may become easier to address with the availability of this technique. However, it is equally important to make sure that the technique is based on good scientific technique.

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[3]Edward Brothers, 3 Sunset West, Ithaca, NY 14850, pers. commun. September 1983.

LITERATURE CITED

ANONYMOUS.
1982. Report on an Otolith Workshop in Bergen, January 18-29, 1982. Dep. Fish. Biol., Univ. Bergen and Inst. Mar. Res., Bergen, Norway, 28 p.

ARMSTRONG, P. B., AND J. S. CHILD.
1965. Stages in the normal development of *Fundulus heteroclitus*. Biol. Bull. (Woods Hole) 128:143-168.

BARKMAN, R. C.
1978. The use of otolith growth rings to age young Atlantic silversides, *Menidia menidia*. Trans. Am. Fish. Soc. 107: 790-792.

BARKMAN, R. C., D. A. BENGTSON, AND A. B. BECK.
1981. Daily growth of the juvenile fish (*Menidia menidia*) in the natural habitat compared with juveniles reared in the laboratory. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178: 324-326.

BARKMANN, R. C., AND A. BECK.
1976. Incubating eggs of the Atlantic silverside on nylon screen. Prog. Fish-Cult. 38:148-150.

BLAXTER, J. H. S.
1969. Development: eggs and larvae. *In* W. S Hoar and D. J. Randall (editors), Fish physiology, Vol. III, p. 177-252. Acad. Press, N.Y.

BROTHERS, E. B.
1978. Exogenous factors and the for...ation of daily and subdaily growth increments in fish otoliths. [Abstr.] Am. Zool. 18:631.

BROTHERS, E. B., E. D. PRINCE, AND D. W. LEE.
1983. Age and growth of young-of-the-year bluefin tuna, *Thunnus thynnus*, from otolith microstructure. *In* E. D. Prince and L. M. Pulos (editors), Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, billfishes, and sharks, p. 49-59. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8.

BROTHERS, E. B., C. P. MATHEWS, AND R. LASKER.
1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U.S. 74:1-8.

BROTHERS, E. B., AND W. N. MCFARLAND.
1981. Correlations between otolith microstructure, growth, and life history transitions in newly recruited french grunts [*Haemulon flavolineatum* (demarest) Haemulidae]. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:369-374.

CAMPANA, S. E., AND J. D. NEILSON.
1982. Daily growth increments in otoliths of starry flounder (*Platichthys stellatus*) and the influence of some environmental variables in their production. Can. J. Fish. Aquat. Sci. 39:937-942.

DUNKELBERGER, D. G., J. M. DEAN, AND N. WATABE.
1980. The ultrastructure of the otolithic membrane and otolith in the juvenile mummichog, *Fundulus heteroclitus*. J. Morphol. 163:367-377.

GEFFEN, A. J.
1982. Otolith ring deposition in relation to growth rate in the herring (*Clupea harengus*) and turbot (*Scophthalmus maximus*) larvae. Mar. Biol. (Berl.) 71:317-326.
1983. The deposition of otolith rings in Atlantic salmon, *Salmo salar* L., embryos. J. Fish Biol. 23:467-474.

GJØSAETER, H.
1981. Dagsonelesing som metode i aldersstudier pa fisk, med eksempler pa anvendelse pa tropiske og boreale arter. Ph.D. Thesis, Univ. Bergen, Bergen, Norway, 172 p.

GJØSAETER, H., AND V. ØIESTAD.
1981. Growth patterns in otoliths as an indication of daily growth variations of larval herring (*Clupea harengus*) from an experimental ecosystem. ICES C.M. 1981/H:31.

GJØSAETER, H., AND S. TILSETH.
1981. Primary growth increments in otoliths of cod larvae (*Gadus morhua* L.) of the arcto-norwegian cod stock. Fisk. Dir. Skr. Ser. Havunders. 17:287-295.

GRAHAM, J. J., AND B. J. JOULE.
1981. Preliminary evaluation of the 1980 larval year class strength of coastal Maine herring. N.A.F.O. (Northwest Atl. Fish. Organ.), Sci. Counc. Rep. Doc. 81/IX/140, 22 p.

JONES, C. M.
1984. The otolith increment technique: Application in larval fish. Ph.D. Thesis, Univ. Rhode Island, Kingston, 123 p.
1985. Within-season differences in growth of larval herring, *Clupea harengus*. Fish. Bull., U.S. 83:289-298.

LAROCHE, J. L., S. L. RICHARDSON, AND A. A. ROSENBERG.
1982. Age and growth of a pleuronectid, *Parophrys vetulus*, during the pelagic larval period in Oregon coastal waters. Fish. Bull., U.S. 80:93-104.

LASKER, R.
1964. An experimental study of the effect of temperature on the incubation time, development, and growth of Pacific sardine embryos and larvae. Copeia 1964:399-405.

LAURENCE, G. C., T. A. HALAVIK, B. R. BURNS, AND A. S. SMIGIELSKI.
1979. An environmental chamber for monitoring "in situ" growth and survival of larval fishes. Trans. Am. Fish. Soc. 108:197-203.

LOUGH, R. G., M. PENNINGTON, G. R. BOLZ, AND A. A. ROSENBERG.
1982. Age and growth of larval Atlantic herring, *Clupea harengus* L., in the Gulf of Maine-Georges Bank region based on otolith growth increments. Fish. Bull., U.S. 80:187-199.

MARSHALL, S. L., AND S. S. PARKER.
1982. Pattern identification in the microstructure of sockeye salmon (*Oncorhynchus nerka*) otoliths. Can. J. Fish. Aquat. Sci. 39:542-547.

METHOT, R. D., JR.
1983. Seasonal variation in survival of larval northern anchovy, *Engraulis mordax*, estimated from the age distribution of juveniles. Fish. Bull., U.S. 81:741-750.

METHOT, R. D., JR., AND D. KRAMER.
1979. Growth of the northern anchovy, *Engraulis mordax*, larvae in the sea. Fish. Bull., U.S. 77:413-423.

NEILSON, J. D., AND G. H. GEEN.
1982. Otoliths of chinook salmon (*Oncorhynchus tshawytscha*): Daily growth increments and factors influencing their production. Can. J. Fish. Aquat. Sci. 39:1340-1347.

ØIESTAD, V.
1982. Application of enclosures to studies on the early life history of fishes. *In* G. D. Grice and M. R. Reeve (editors), Marine Mesocosms, p. 49-62. Springer-Verlag, N.Y.

PANNELLA, G.
1971. Fish otoliths: daily growth layers and periodic patterns. Science 173:1124-1127.
1974. Otolith growth patterns: an aid in age determination in temperate and tropical fishes. *In* T. B. Bagenal (editor), The Proceedings of an International Symposium on the Aging of Fish, p. 28-39. Unwin Brothers, Surrey, Engl.

RADTKE, R. L.
1978. The formation and growth of otoliths in the estuarine fish, *Fundulus heteroclitus*. Ph.D. Thesis, Univ. South Carolina, Columbia, 57 p.
1980. The formation and growth of otoliths from redfish (*Sebastes* spp.) larvae from the Flemish Cap (Division 3M). N.A.F.O. (Northwest Atl. Fish. Organ.), Sci. Counc. Rep. Doc. 80/IX/153 Ser. N225, 5 p.
1984. Formation and structural composition of larval striped

mullet otoliths. Trans. Am. Fish. Soc. 113:186-191.

RADTKE, R. L., AND J. M. DEAN.
1982. Increment formation in the otoliths of embryos, larvae, and juveniles of the mummichog, *Fundulus heteroclitus*. Fish. Bull., U.S. 80:201-215.

RADTKE, R. L., AND M. D. SCHERER.
1982. Daily growth of winter flounder (*Pseudopleuronectes americanus*) larvae in the Plymouth Harbor estuary. *In* Proceedings of the Fifth Annual Larval Fish Conference, p. 1-5. Louisiana Cooperative Fishery Research Unit, Louisiana State University, Baton Rouge, LA.

RADTKE, R. L., AND K. G. WAIWOOD.
1980. Otolith formation and body shrinkage due to fixation in larval cod (*Gadus morhua*). Can. Tech. Rep. Fish. Aquat. Sci. No. 929, 10 p.

RALSTON, S., AND G. T. MIYAMOTO.
1983. Analyzing the width of daily otolith increments to age the Hawaiian snapper, *Pristipomoides filamentosus*. Fish. Bull., U.S. 81:523-535.

RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull 191, 382 p.

ROSENBERG, A. A., AND A. S. HAUGEN.
1983. Individual growth and size-selective mortality of larval turbot (*Scophthalmus maximus*) reared in enclosures. Mar. Biol. (Berl.) 72:73-77.

ROSENBERG, A. A., AND J. L. LAROCHE.
1982. Growth during metamorphosis of English sole, *Parophrys vetulus*. Fish. Bull., U.S. 80:150-153.

SCHMIDT, R. E., AND M. C. FABRIZIO.
1980. Daily growth rings on otoliths for aging young-of-the-year largemouth bass from a wild population. Prog. Fish-Cult. 42:78-80.

SCOTT, J. S.
1973. Otolith structure and growth in northern sand lance, *Ammodytes dubius*, from the Scotian shelf. Int. Comm. Northwest Atl. Fish., Res. Bull. 10, p. 107-115.

SMIGIELSKI, A. S., AND C. R. ARNOLD.
1972. Separating and incubating winter flounder eggs. Prog. Fish-Cult. 34:113.

STEFFENSEN, E.
1980. Daily growth increments observed in otoliths from juvenile East Baltic cod. Dana 1:29-37.

STRUHSAKER, P., AND J. H. UCHIYAMA.
1976. Age and growth of the nehu, *Stolephorus purpureus* (Pisces: Engraulidae), from the Hawaiian Islands as indicated by daily growth increments of sagittae. Fish. Bull., U.S. 74:9-17.

TANAKA, K., Y. MUGIYA, AND J. YAMADA.
1981. Effects of photoperiod and feeding on daily growth patterns in otoliths of juvenile *Tilapia nilotica*. Fish. Bull., U.S. 79:459-466.

TAUBERT, B. D., AND D. W. COBLE.
1977. Daily rings of otoliths of three species of *Lepomis* and *Tilapia mossambica*. J. Fish. Res. Board Can. 34:332-340.

TOWNSEND, D. W., AND J. J. GRAHAM.
1981. Growth and age structure of larval Atlantic herring, *Clupea harengus harengus*, in the Sheepscot River estuary, Maine, as determined by daily growth increments in otoliths. Fish. Bull., U.S. 79:123-130.

TSUJI, S., AND T. AOYAMA.
1982. Daily growth increments observed in otoliths of the larvae of Japanese Red Sea bream *Pagrus major* (Temminch et Schlegel). Bull. Jpn. Soc. Sci. Fish. 48:1559-1562.

VICTOR, B. C.
1982. Daily otolith increments and recruitment in two coral-reef wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*. Mar. Biol. (Berl.) 71:203-208.
1983. Recruitment and population dynamics of a coral reef fish. Science 219:419-420.

VOLK, E. C., R. C. WISSMAR, C. A. SIMENSTAD, AND D. M. EGGERS.
1984. Relationship between otolith microstructure and the growth of juvenile chum salmon (*Oncorhynchus keta*) under different prey rations. Can. J. Fish. Aquat. Sci. 41:126-133.

WATABE, N., K. TANAKA, J. YAMADA, AND J. M. DEAN.
1982. Scanning electron microscope observations of the organic matrix in the otolith of the teleost fish *Fundulus heteroclitus* (Linnaeus) and *Tilapia nilotica* (Linnaeus). J. Exp. Mar. Biol. Ecol. 58:127-134.

WILSON, K. H., AND P. A. LARKIN.
1980. Daily growth rings in the otoliths of juvenile sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 37:1495-1498.
1982. Relationship between thickness of daily growth increments in sagittae and change in body weight of sockeye salmon (*Oncorhynchus nerka*) fry. Can. J. Fish. Aquat. Sci. 39:1335-1339.

PATTERNS IN DISTRIBUTION AND ABUNDANCE OF A NONCOEVOLVED ASSEMBLAGE OF ESTUARINE FISHES IN CALIFORNIA

PETER B. MOYLE,[1] ROBERT A. DANIELS,[2] BRUCE HERBOLD,[1] AND DONALD M. BALTZ[3]

ABSTRACT

The patterns of distribution and abundance of the fishes of Suisun Marsh, a portion of the Sacramento-San Joaquin estuary in central California, were studied over a 54-month period. Total fish abundance in the marsh exhibited strong seasonality; numbers and biomass were lowest in winter and spring and highest in late summer. Freshwater inflow was highest in the winter and lowest in late summer, when salinities and temperatures were highest. Twenty-one species were collected on a regular basis; the 10 most abundant were *Morone saxatilis, Pogonichthys macrolepidotus, Gasterosteus aculeatus, Hysterocarpus traski, Cottus asper, Spirinchus thaleichthys, Acanthogobius flavimanus, Catostomus occidentalis, Leptocottus armatus,* and *Platichthys stellatus.* Another 21 species occurred in small numbers on an irregular basis. Twenty of the 42 species had been introduced to California since 1879. Of the 21 common species, 14 were residents, 4 were winter seasonals, and 3 were spring/summer seasonals. The resident species fell into two groups: a group of native species that were concentrated in small dead-end sloughs and a group of native and introduced species that were most abundant in the larger sloughs. The seasonal species were also a mixture of native and introduced species. Total fish abundance and species diversity declined through the study period, which seemed to be related to strong year classes of some species early in the study and the prevalance of freshwater conditions late in the study. The structure of the fish assemblage was fairly consistent over the study period but changes are expected in the near future. The structure of the Suisun Marsh fish assemblage was similar to that found in other river-dominated estuaries, despite the mixture of native and introduced species.

The Sacramento-San Joaquin Estuary system is the largest estuary on the west coast of North America. It has been highly modified by surrounding urban, industrial, and agricultural development and by extensive diversion and pollution of the freshwater that flows into it (Conomos 1979). It supports a diverse fish fauna of native and introduced species, but most previous studies have concentrated on species important to sport and commercial fisheries, especially striped bass, *Morone saxatilis,* and, to a much lesser extent, white sturgeon, *Acipenser transmontanus;* chinook salmon, *Oncorhynchus tshawytscha;* American shad, *Alosa sapidissima;* and white catfish, *Ictalurus catus* (Skinner 1972; Moyle 1976). Studies of other species have been few (Ganssle 1966; Turner and Kelley 1966; Baltz and Moyle 1982; Stevens and Miller 1983; Daniels and Moyle 1983), and there have been no community-level analyses equivalent to those conducted on estuarine fish communities in other parts of the world (e.g., Dahlberg and Odum 1970; Livingston 1976; Sheridan and Livingston 1979; Meeter et al. 1979; Blaber and Blaber 1980; Quinn 1980; Thorman 1982). The fish assemblage of the Sacramento-San Joaquin Estuary system is unusual because few of its component species are likely to have evolved together; it is composed of a mixture of introduced and native freshwater, estuarine, and euryhaline marine species (Table 1). The introduced species come from a number of geographic areas, while most of the native species have their centers of abundance in either the rivers upstream or the saltwater bays downstream from the estuary. There are no really comparable estuaries on the California coast, although some of the much smaller and more saline estuaries south of the Sacramento-San Joaquin Estuary do have fish assemblages composed in part of introduced species (Allen 1982).

We began in January 1979 systematic sampling of the fishes in Suisun Marsh on a monthly basis. Suisun Marsh was chosen as a study site because of its central location on the estuary, its proximity to the University of California, Davis campus, and the availability of earlier data from sporadic sampling by the California Department of Fish and Game. The data indicated that the fish fauna was typical of the

[1]Wildlife and Fisheries Biology, University of California, Davis, CA 95616.

[2]Wildlife and Fisheries Biology, University of California, Davis, CA; present address: Biological Survey, New York State Museum, Albany, NY 12230.

[3]Wildlife and Fisheries Biology, University of California, Davis, CA; present address: Coastal Fisheries Institute, Louisiana State University, Baton Rouge, LA 70803.

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TABLE 1.—Fishes collected in Suisun Marsh, Solono County, CA, in decreasing order of numerical abundance in our trawls. The principal environment of each species is coded as follows: A = anadromous, E = estuarine, F = freshwater, M = marine.

Species	Numbers	Origin
Striped bass, *Morone saxatilis*	24,154	E. North America (E)
Splittail, *Pogonichthys macrolepidotus*	11,250	Native (E)
Threespine stickleback, *Gasterosteus aculeatus*	9,956	Native (F-E)
Tule perch, *Hysterocarpus traski*	7,693	Native (F-E)
Prickly sculpin, *Cottus asper*	4,639	Native (F-E)
Yellowfin goby, *Acanthogobius flavimanus*	1,786	Japan (E-M)
Sacramento sucker, *Catostomus occidentalis*	1,703	Native (F)
Common carp, *Cyprinus carpio*	1,573	Asia (F)
Threadfin shad, *Dorosoma petenense*	1,088	E. North America (E)
Staghorn sculpin, *Leptocottus armatus*	985	Native (M)
Starry flounder, *Platichthys stellatus*	849	Native (M)
Longfin smelt, *Spirinchus thaleichthys*	650	Native (E)
Delta smelt, *Hypomesus transpacificus*	450	Native (E)
American shad, *Alosa spadissima*	218	E. North America (A)
Sacramento squawfish, *Ptychocheilus grandis*	140	Native (F)
Chinook salmon, *Oncorhynchus tshawytscha*	96	Native (A)
Hitch, *Lavinia exilicauda*	56	Native (F)
Inland silverside, *Menidia beryllina*	50	E. North America (F-E)
Goldfish, *Carassius auratus*	45	Asia (F)
Northern anchovy, *Engraulis mordax*	34	Native (M)
Sacramento blackfish, *Orthodon microlepidotus*	25	Native (F)
Pacific herring, *Clupea harengeus*	24	Native (M)
White catfish, *Ictalurus catus*	23	E. North America (F)
Bluegill, *Lepomis macrochirus*	16	E. North America (F)
Mosquitofish, *Gambusia affinis*	15	E. North America (F)
Black crappie, *Pomoxis nigromaculatus*	14	E. North America (F)
Bigscale logperch, *Percina macrolepida*	10	Texas (F)
White sturgeon, *Acipenser transmontanus*	10	Native (E)
Fathead minnow, *Pimephales promelas*	9	E. North America (F)
Brown bullhead, *Ictalurus nebulosus*	6	E. North America (F)
Rainwater killifish, *Lucania parva*	5	E. North America (E)
Green sunfish, *Lepomis cyanellus*	4	E. North America (F)
Pacific sanddab, *Citharichthys sordidus*	4	Native (M)
Pacific lamprey, *Lampetra tridentata*	4	Native (A)
Surf smelt, *Hypomesus pretiosus*	3	Native (M)
Channel catfish, *Ictalurus punctatus*	3	E. North America (F)
Black bullhead, *Ictalurus melas*	3	E. North America (F)
Shiner perch, *Cymatogaster aggregata*	3	Native (M)
Golden shiner, *Notemigonus crysoleucus*	3	E. North America (F)
Warmouth, *Lepomis gulosus*	1	E. North America (F)
Rainbow trout, *Salmo gairdneri*	1	Native (A)
Longjaw mudsucker, *Gillichthys mirabilis*	1	Native (M)

freshwater dominated portions of the estuary. The marsh is also of considerable interest because it is the largest brackish-water marsh in California. It is managed primarily as a wintering area for migratory waterfowl, but its importance as a nursery area for striped bass, salmon, and other fishes is being increasingly recognized (Baracco 1980). The purpose of this paper is to analyze the distribution and abundance of the fishes of the marsh in relation to each other, major environmental factors, and major crustacean species, during a 54-mo period.

STUDY AREA

Suisun Marsh is a large (ca 34,000 ha) tidal marsh located just downstream of the confluence of the Sacramento and San Joaquin rivers (Fig. 1). About 11,000 ha of the marsh consist of sloughs that are influenced by tidal action. The remainder consists of diked wetlands managed to attract wintering waterfowl (Baracco 1980) and for pasturage. The sloughs are shallow (most are <2 m deep) and may fluctuate in depth as much as 1 m during extreme tides. Salinities have ranged from 0 to nearly 17 ppt in recent years, with the highest salinities occurring in late summer of drought years and the lowest salinities occurring annually in winter and spring when river outflows are highest (Baracco 1980). Because increased upstream diversion of water is threatening water quality in the marsh, major modifications to the water distribution system within the marsh are being made to ensure that salinites do not become too high for production of the plants that attract waterfowl.

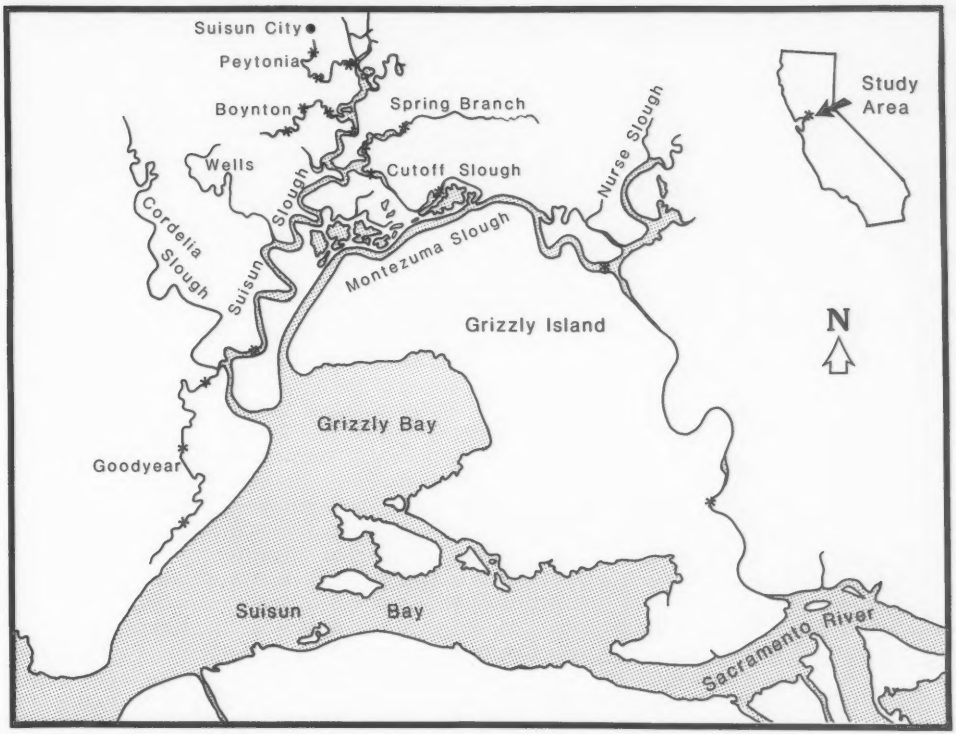

FIGURE 1.—Locations of sample sites (*) in Suisun Marsh, Sacramento-San Joaquin Estuary, CA.

During this study, two major habitat types were sampled: 1) small dead-end sloughs that were 7-10 m wide and 1-2 m deep and 2) Suisun Slough, which connected all the dead-end sloughs and was 100-150 m wide and 2-4 m deep. A third habitat, Montezuma Slough, was also sampled, but the data were not used here because our methods did not sample it adequately. This slough is deep (3-4 m), wide, and riverlike; it is the marsh's main source of freshwater.

METHODS

Sampling was conducted monthly at seven locations throughout the marsh (Fig. 1), from January 1979 through June 1983, with the exception of December 1979 and October 1980. Four of the locations were in dead-end sloughs (Peytonia, Boynton, Mallard, and Goodyear), one was a small slough open at both ends (Cutoff), and two were in Suisun Slough. Sampling was conducted biweekly from January 1980 through June 1981, but the samples for each month were lumped together for analysis, as the samples within months were comparable. All samples were taken during the day, as 24-h studies conducted in April 1979 and 1980 did not exhibit any significant differences between day and night samples.

The principal means of sampling was a four-seam otter trawl with a 1 × 2.5 m opening, a length of 5.3 m, and mesh sizes that tapered down to 6 mm stretch in the bag. At each location, the trawl was towed for either 5 min (small sloughs) or 10 min (Suisun Slough) at about 4 km/h. The longer periods were necessary in large sloughs because of the small catches that prevailed there. Each location was sampled at least twice on each date. This method of sampling was biased because large fishes probably avoided the trawl, and fishes that favor the emergent vegetation were undersampled, as were fishes in the upper part of the water column (Kjelson and Colby 1977). However, these problems were minimized by the narrowness and shallowness of most of the sampling sites; in any case such biases were consis-

tent across the course of this study, so that comparisons should be unaffected. In addition, two locations on the marsh were sampled with a 10 × 1 m, 6 mm mesh, seine, on an irregular basis. An effort was made to seine every month but it was often not possible, as the sites were difficult to seine at extreme high or low tides.

Fishes from each trawl were placed in washtubs of water to minimize mortality and then identified, measured to the nearest millimeter (standard length), and returned to the water as quickly as possible. If more than 100 fish of any one size class of a species were captured, only the first 100 were measured; the rest were counted. Early in the study, samples of all fishes were weighed (wet weight, in gram), and a length/weight relationship developed for each species. This was later used to estimate the biomass of fish in each trawl. The shrimps *Crangon franciscorum* and *Palaemon macrodactylus* in each trawl were also counted. For the oppossum shrimp, *Neomysis mercedis*, an index of abundance was used, based on a 1-to-5 scale, where "1" represented <3 individuals; "2", 3-50 shrimp; "3", 50-200, "4", 200-500, and "5", >500. The index was necessary because most *N. mercedis* probably passed through the net due to their small size (3-5 mm). Nevertheless, they were present seasonally in most hauls, at times in enormous numbers.

At each location, salinity and temperature were taken with a YSI S-C-T meter and transparency was measured with a Secchi disk. Tidal height was determined from a tide table. An index of monthly freshwater outflow from the combined Sacramento and San Joaquin Rivers at Chipps Island was obtained from the California Department of Water Resources (unpubl. data).

For analysis, all the data were summarized by site and month. A Spearman rank correlation analysis using data ranked by month (N = 52) was used for the initial analysis because many of the variables did not conform to a normal distribution. Because no single transformation could be applied to all the variables, nonparametric statistics were used as the most conservative method. We used 13 variables for the analysis (Table 2). In addition, rank abundance (by numbers) by month for the following species categories was used: 1) total striped bass, 2) yearling and older striped bass, 3) young-of-year striped bass, 4) total splittail, 5) yearling and older splittail, 6) young-of-year splittail, 7) total tule perch, 8) tule perch adults, 9) tule perch young-of-year, 10) total prickly sculpin, 11) yearling and older prickly sculpin, 12) prickly sculpin young-of-year, 13) carp, 14) longfin smelt, 15) delta smelt, 16) staghorn sculpin, 17) starry flounder, 18) threadfin shad, 19) Sacramento sucker, 20) yellowfin goby, and 21) threespine stickleback. Because only minor differences were found among the correlations associated with adult and juvenile striped bass, tule perch, splittail, and prickly sculpin, only the results for the totals for these species will be presented.

Analyses were also run using the data from each trawl separately. Species were analyzed using both numbers and grams. Because these data were all of species abundances, a log-normal transformation was used to normalize them. The results were similar in most respects to the analyses using ranks so are not presented here. However, because we were uncertain as to the validity of using ranked data for principal components analysis (PCA), we based our discussion on cautious inspection of the correlation matrix as generated. A principal components analysis was run using the correlation matrix (Dixon and Brown 1977) of l_n numbers of fish per trawl (N = 1,238), to produce groups of species that presumably were responding to the environment in the same general ways.

TABLE 2.—Environmental variables used in the correlation analyses.

Variable	Units	Notes
Month series	1-54	January 1979 to June 1983
Water year	1-5	Begins in October of each year
Salinity	ppt	
Temperature	°C	
Secchi depth	cm	
Neomysis mercedis abundance	1-5 index	
Mean monthly outflow	0-11 index	California Department of Water Resources
Crangon franciscorum	No./trawl	
Palaemon macrodacytlus	No./trawl	
Fish species	No./trawl	
Total fish numbers	No./trawl	
Total fish biomass	Biomass/trawl	Wet weight
Species diversity	Index	Shannon-Weiner (H)

RESULTS

Environmental Variables

Salinity and temperature were negatively correlated with river outflows (Table 3, Fig. 2). Salinity had a strong ($P < 0.01$) positive correlation only with Secchi depth. River outflows generally peaked in February, March, or April, as the result of run-off from melting snow in the Sierra Nevada. Lowest

TABLE 3.—Spearman rank correlation coefficients between fish species ranked by month by numbers and other variables ranked by month. Underlined values are significant at $P > 0.05$.

	Striped bass	Splittail	Tule perch	Sacramento sucker	Yellowfin goby	Carp	Prickly sculpin	Stickleback	Delta smelt	Longfin smelt	Threadfin shad	Staghorn sculpin	Starry flounder
Month series	−0.42	−0.72	−0.51	−0.38	−0.53	−0.58	0.16	−0.10	−0.29	−0.09	−0.26	−0.15	−0.21
Temperature	0.54	0.28	0.08	0.21	0.49	0.49	0.41	−0.33	−0.41	−0.28	−0.55	−0.03	0.01
Salinity	0.62	0.24	0.53	0.14	0.43	0.38	−0.36	−0.14	0.18	0.17	0.24	0.13	−0.06
Secchi depth	0.09	−0.09	0.29	−0.18	−0.08	−0.04	−0.54	−0.09	0.33	0.31	0.52	0.06	−0.28
Outflow	−0.74	−0.36	−0.49	−0.27	−0.62	−0.44	0.06	0.04	0.07	−0.12	0.16	−0.06	0.14
Neomysis mercedis	−0.42	−0.02	−0.24	0.09	−0.45	−0.05	0.28	0.23	0.07	−0.25	−0.10	0.07	0.08
Crangon franciscorum	0.27	−0.01	0.05	0.06	0.46	−0.18	−0.03	−0.10	0.01	−0.59	−0.15	0.29	−0.23
Palaemon macrodactylus	0.43	−0.10	0.06	−0.10	0.34	0.20	0.16	−0.18	−0.30	−0.21	−0.32	0.14	0.23
No./trawl	0.67	0.64	0.72	0.53	0.46	0.45	0.07	0.21	0.16	−0.07	0.06	−0.18	−0.10
g/trawl	0.39	0.71	0.53	0.57	0.39	0.81	−0.06	−0.13	0.04	−0.24	0.13	0.04	0.04
Species/trawl	0.42	0.74	0.48	0.56	0.60	0.52	0.24	0.10	0.21	0.15	0.00	0.21	0.43
Diversity (H′)	−0.10	0.45	0.23	0.45	0.28	0.35	0.31	0.21	0.26	0.09	0.12	0.36	0.43

flows occurred from August through October. Salinity, temperature, and Secchi depth were generally lowest (0-1 ppt, 8°-11°C, and 17-18 cm, respectively) when outflows were highest, and highest (4-9 ppt, 19°-23°C, and 25-40 cm, respectively when outflows were lowest. There is, however, considerable year-to-year variation in these cycles. When outflows were comparatively low (1979, 1981), salinities, temperatures, and turbidities peaked at higher levels than they did in high outflow years. Because 1982 and 1983 were exceptionally wet years, virtual freshwater conditions prevailed throughout both years.

Invertebrates

Neomysis mercedis became very abundant in the marsh from April to June, but the population declined rapidly through the summer, reaching a low in October (Fig. 2). This pattern fits with previous studies of this species, which showed that its populations generally followed the mixing zone up and down the estuary and were reduced at temperatures higher then 22°C and salinities >7 ppt (Orsi and Knutson 1979). In this study, *N. mercedis* abundance showed a significant positive correlation with outflows and significant negative correlations with temperature, salinity, and turbidity (Table 4). It also showed a significant negative correlation (Table 3) with two of its major predators in the marsh, striped bass and yellowfin goby (Herbold 1985[4]).

Palaemon macrodactylus and *Crangon franciscorum* also showed seasonal patterns of abundance (Sigfreid 1980), but the patterns were much less marked than those of *N. mercedis*. *Palaemon macrodactylus* were most abundant during July through October and least abundant during January and February, while *C. franciscorum* were most abundant in November and December and least abundant in January through March. *Palaemon macrodactylus* abundance therefore showed strong positive correlation with temperature and salinity and a negative correlation with outflows. *Crangon franciscorum* abundance was also negatively correlated with outflows, but had a positive correlation only with salinity.

Fishes

A total of 42 species, represented by about 67,000 individuals, were collected in the 1,238 trawl hauls made during the study. The four measures of overall fish abundance and diversity showed negative correlations with month series and with years, indicating a general decline through the study period (Table 4, Fig. 3). Numbers, biomass, and number of species had positive correlations with temperature and/or salinity and negative correlations with out-

[4]Herbold, B. 1985. Resource partitioning within a non-coevolved assemblage of fishes. Unpubl. Ph.D. Thesis, Univ. California, Davis.

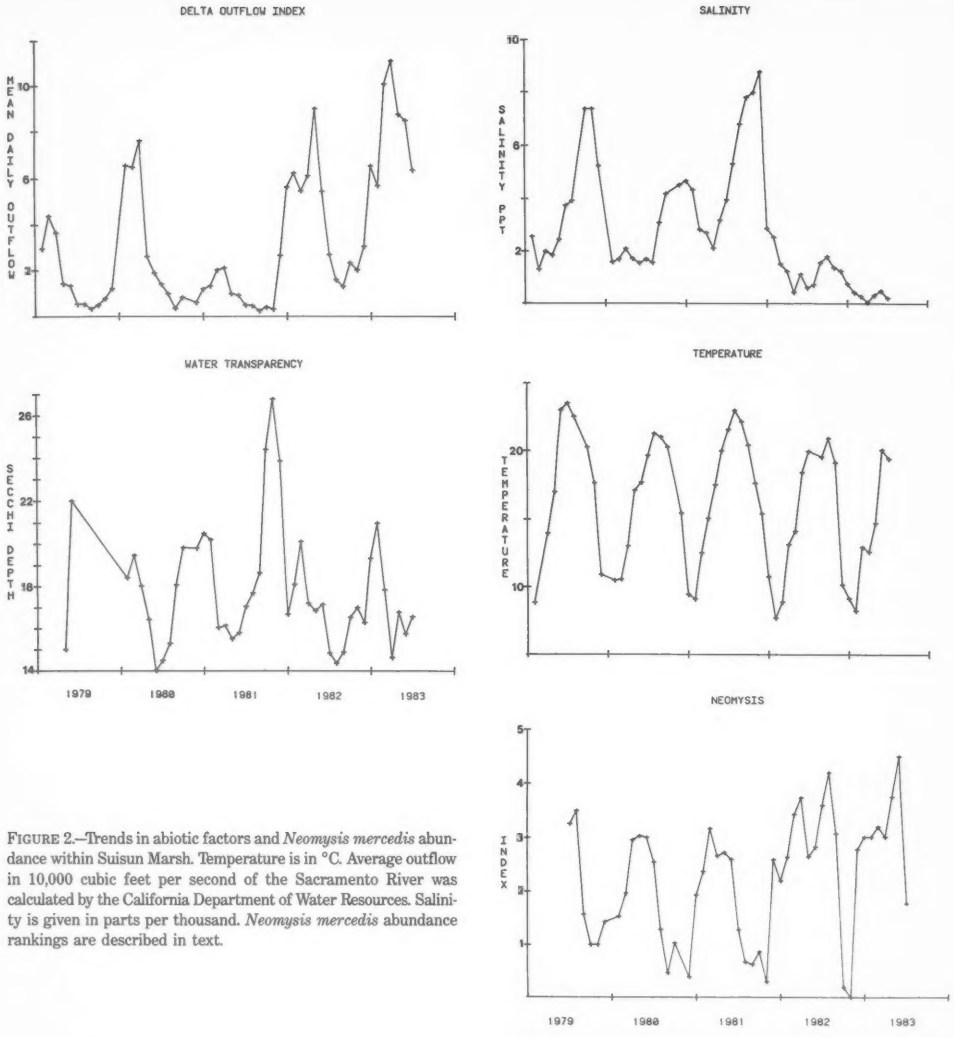

FIGURE 2.—Trends in abiotic factors and *Neomysis mercedis* abundance within Suisun Marsh. Temperature is in °C. Average outflow in 10,000 cubic feet per second of the Sacramento River was calculated by the California Department of Water Resources. Salinity is given in parts per thousand. *Neomysis mercedis* abundance rankings are described in text.

flow, indicating that catches were highest in late summer and lowest in early spring. However, when the patterns of occurrence of the 12 most abundant species were examined, three groups appeared: resident species, winter seasonals, and spring/summer seasonals.

The "resident species" included the native splittail, tule perch, Sacramento sucker, prickly sculpin, and threespine stickleback as well as the introduced striped bass, carp, and yellowfin goby. Two additional species, native white sturgeon and introduced American shad, probably also belonged in this category, as they were caught at all times of the year but too infrequently to draw any firm conclusions. Splittail, striped bass, tule perch, Sacramento sucker, carp, and yellowfin goby had similar patterns of abundance (Figs. 4, 5) and were correlated ($P < 0.05$) with each other and with total biomass, numbers, and species (Tables 3, 4). All six species usually became more abundant in our catches as the sum-

TABLE 4.—Spearman rank correlation among species ranked by month (lower matrix) by numbers and among environmental and other variables ranked by month (upper matrix). Underlined values are significant at $P > 0.05$.

	1	2	3	4	5	6	7	8	9	10	11	12	
13. Striped bass		−0.15	−0.54	−0.10	0.43	0.14	−0.04	−0.04	−0.51	−0.79	−0.80	−0.64	1. Month series
14. Splittail	0.50		0.27	0.19	−0.62	−0.29	0.19	0.44	0.33	0.30	0.37	0.05	2. Temperature
15. Tule perch	0.44	0.38		0.46	−0.78	−0.55	0.42	0.32	0.48	0.37	0.39	0.07	3. Salinity
16. Sacramento sucker	0.19	0.51	0.54		−0.13	−0.43	0.04	−0.24	0.01	0.01	−0.11	−0.19	4. Secchi depth
17. Yellowfin goby	0.68	0.58	0.32	0.22		0.51	−0.52	−0.41	−0.58	−0.34	−0.51	−0.06	5. Outflow
18. Carp	0.46	0.53	0.38	0.46	0.35		−0.56	−0.32	−0.14	−0.03	−0.10	0.16	6. *Neomysis*
19. Prickly sculpin	−0.14	0.13	−0.13	0.34	0.06	0.11		0.34	0.09	−0.19	0.25	0.01	7. *Crangon*
20. Stickleback	−0.41	−0.09	0.05	0.07	−0.22	−0.17	0.09		0.12	0.04	0.15	−0.05	8. *Palaemon*
21. Delta smelt	−0.11	0.08	0.21	0.03	−0.05	−0.15	−0.15	0.40		0.55	0.56	−0.08	9. Numbers/ trawl
22. Longfin smelt	−0.07	−0.01	−0.09	−0.12	0.21	−0.38	−0.15	−0.04	0.43		0.69	0.51	10. Grams/trawl
23. Threadfin shad	−0.17	−0.02	0.38	0.00	−0.24	−0.11	−0.47	0.42	0.36	0.21		0.74	11. Species/trawl
24. Staghorn sculpin	−0.24	−0.13	−0.05	0.06	−0.06	−0.02	0.20	0.18	0.17	0.30	0.01		12. Diversity (H′)
25. Starry flounder	−0.09	0.30	0.03	0.30	0.18	−0.14	0.25	0.22	0.10	0.37	0.00	0.07	
	13	14	15	16	17	18	19	20	21	22	23	24	

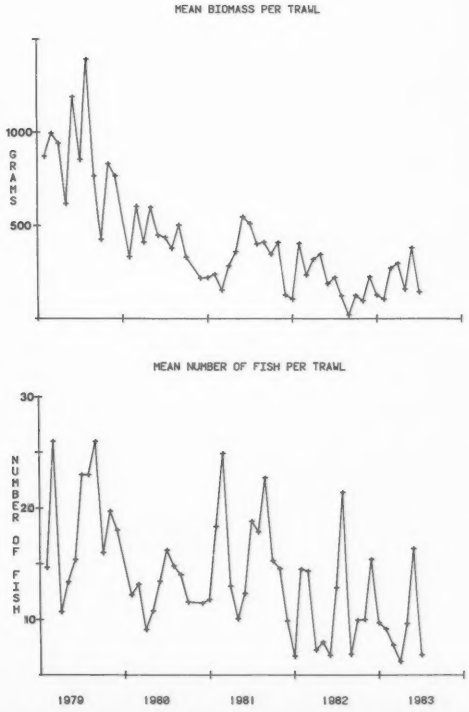

FIGURE 3.—Trends in mean numbers and grams of fish per trawl.

mer progressed although the two introduced species, striped bass and yellowfin goby, tended to peak later than the other species. Consequently, they all showed significant ($P < 0.05$) negative correlations with outflow. All except Sacramento sucker and tule perch had significant positive correlations with salinity and temperature. There was a general decline in fish abundance throughout the 5-yr period. This was reflected in that four of the six species showed a positive correlation with species diversity, and all had a negative correlation with month series.

Prickly sculpin seemed to peak in abundance earlier in the year than the first six species (Fig. 4) but the pattern was obscured by the considerable year-to-year variation in abundance of young-of-year fish. Adults were resident in the marsh but appeared in the trawls on an irregular basis because of their tendency to hide under logs and other objects (Moyle 1976). Overall, prickly sculpin had negative correlations with salinity and Secchi depth, but positive correlations with temperature, *N. mercedis* abundance, and species diversity (Table 3). Threespine stickleback abundance had a negative correlation only with temperature, presumably because their reproductive behavior obscured our ability to catch them. They were most abundant in the trawls in February through May, and the catch consisted primarily of gravid females and schools of young-of-year fish. The males were apparently defending their nesting territories in emergent vegetation. By late summer sticklebacks were rare in the trawls but could be taken in seine hauls made through weedy areas.

The "winter seasonals" were three plankton-

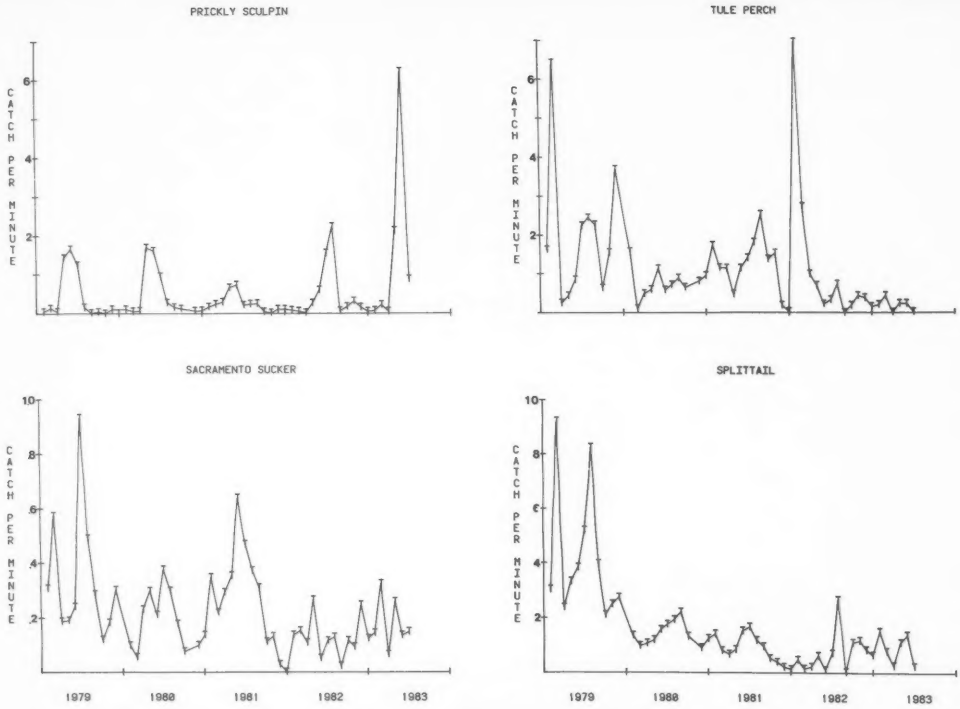

FIGURE 4.—Capture rates of native resident species within Suisun Marsh. Mean catch per effort is described as percent of the total catch for each species.

feeding species, delta smelt (native), longfin smelt (native), and threadfin shad (introduced). All three species tended to be most abundant in November through January, although the pattern was not always consistent (Fig. 6). Threadfin shad were the most erratic of the three species in abundance; they were especially abundant in the summer of 1981. Longfin smelt were largely absent from our samples in 1979 and 1981. Delta smelt abundance was positively correlated ($P < 0.05$) with that of the other two species, although the correlation between longfin smelt and threadfin shad was not significant. All three species had negative correlations with temperature, and positive correlations with Secchi depth.

The "spring/summer seasonals" were staghorn sculpin and starry flounder, both euryhaline marine species that were represented mainly by young-of-year. Their patterns of abundance were not consistent (Fig. 6) and the peaks occurred anytime from March through September. Consequently, staghorn sculpin did not show any significant correlations with the environmental variables, although starry flounder did show negative correlation with Secchi depth. Both species had a positive correlation with species diversity, presumably because they were rare in our samples during the last 2 years when the marsh was dominated by freshwater.

In addition to the 12 species that appeared regularly in our trawls, there were a number of other species of potential importance to the fish community that were either not sampled adequately by the trawl or were absent because of the effects of the 1976-77 drought. Five species that were not sampled adequately were inland silverside, chinook salmon, Sacramento squawfish, mosquitofish, and rainwater killifish. The silversides were abundant year around in the shallow, sandy or weedy areas found in some sloughs. Silversides appeared in seine hauls in 20 of the 22 mo in which seining was done; they were generally the most abundant fish in these hauls. Juvenile chinook salmon and squawfish were com-

mon in the marsh in February, March, and April (times of high outflows) and were taken mainly in seines. The tendency of the salmon to remain close to the banks and vegetation and to get sucked into diversions of marsh water consequently has led to the screening of one major diversion in the marsh. Squawfish were abundant in the Sacramento River and juveniles are known to disperse widely during high flows (Smith 1982). Mosquitofish and rainwater killifish were present in ponds adjacent to the sloughs, along with silversides and sticklebacks; mosquitofish were planted in some areas for mosquito control.

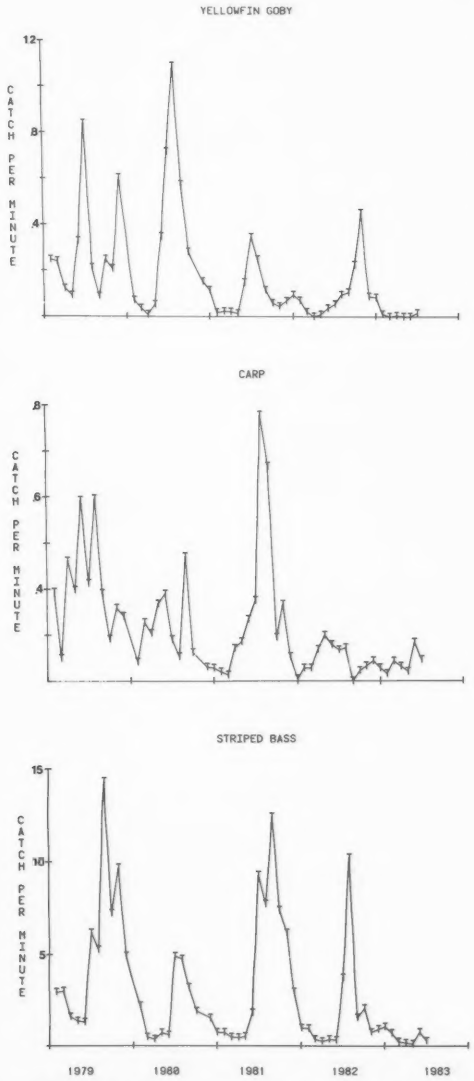

FIGURE 5.—Capture rates of introduced species within Suisun Marsh. Mean catch per effort is described as percent of the total catch for each species.

Principal Components' Analysis

The PCA using the numbers per trawl matrix resulted in four components that explained 47% of the variance in the matrix (Table 5). The first component loaded most heavily on tule perch, Sacramento sucker, and splittail, native resident species most abundant in dead-end sloughs, and to a lesser extent on carp and threadfin shad, introduced species common in such sloughs. The second component loaded heavily on striped bass, yellowfin goby, and carp, three introduced species resident throughout the marsh but most frequently captured in the main sloughs; all reached peaks of abundance in late summer. The third component loaded most heavily on prickly and staghorn sculpins, two benthic species that peaked in abundance during the summer months but were relatively scarce during the last 2

TABLE 5.—Loadings (rotated) of major fish species on four components produced by a principal components analysis of numbers of fish per trawl (n = 1,238). Values over 0.500 are underlined.

	Component 1	Component 2	Component 3	Component 4
Splittail adults	0.487	0.300	−0.024	−0.149
Splittail juveniles	0.549	0.100	0.318	0.149
Striped bass adults	0.058	0.701	0.078	−0.073
Striped bass juveniles	0.183	0.631	−0.157	0.046
Longfin smelt	−0.124	0.029	−0.032	0.747
Delta smelt	0.022	−0.061	−0.027	0.734
Threadfin shad	0.447	−0.286	−0.121	0.319
Common carp	0.403	0.403	0.166	−0.084
Yellowfin goby	−0.011	0.660	0.023	0.016
Tule perch adults	0.827	0.049	0.085	−0.102
Tule perch juveniles	0.833	−0.036	−0.045	−0.017
Sculpin adults	0.254	−0.038	0.377	−0.263
Sculpin juveniles	0.090	0.043	0.780	−0.077
Starry flounder	0.117	0.256	0.107	−0.030
Staghorn sculpin	0.043	0.047	0.727	0.118
Sacramento sucker	0.637	0.197	0.341	0.102
Threespine stickleback	0.039	−0.296	0.486	−0.147
Eigenvalue	2.826	1.874	1.829	1.391
Cumulative proportion of variance explained	0.200	0.304	0.396	0.472

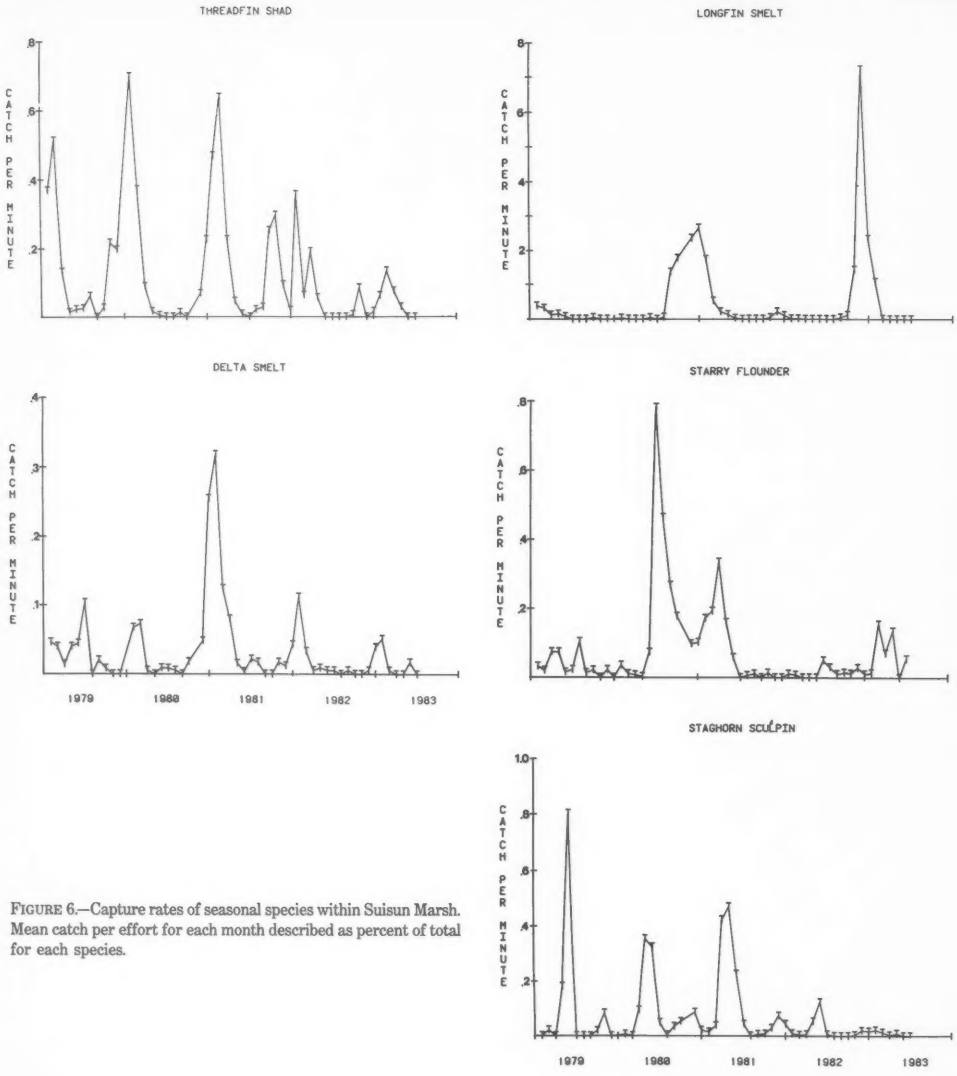

FIGURE 6.—Capture rates of seasonal species within Suisun Marsh. Mean catch per effort for each month described as percent of total for each species.

years of the study. A similar pattern was shown by threespine stickleback, which also had a relatively large positive loading on this component. The fourth component loaded heavily on delta and longfin smelt, and to a lesser extent on threadfin shad. This is the winter seasonal group identified in the previous analysis.

DISCUSSION

During the 5-yr study period, the fish assemblage of Suisun Marsh had the following characteristics:

1. There was a strong seasonal pattern of total fish

abundance with numbers and biomass lowest in winter and spring and highest in late summer. Fishes were least abundant when river outflows were highest and most abundant when salinities and temperatures were highest.

2. There was an overall decline in fish abundance and species diversity through the study period.

3. Of the 21 species that occurred in the marsh on a regular basis, 14 were residents, 4 were winter seasonals, and 3 were spring/summer seasonals. Another 21 species occurred sporadically, in small numbers. These were mainly marine and freshwater species that presumably could become established in the marsh if environmental conditions changed significantly.

4. The abundant resident species fell into two groups, one made up of native species that concentrated in the small dead-end sloughs and the other a mixture of introduced and native species that were widely distributed in the marsh, but most abundant in the larger sloughs.

5. The structure of the fish assemblage (i.e., the pattern of distribution and abundance) was fairly consistent over the 54-mo period.

The seasonal pattern of fish abundance was due to a number of factors, most importantly 1) variation in sampling efficiency, 2) influxes of young-of-year fish, 3) favorable environmental conditions for most fish species in late summer, and 4) abundance of *Neomysis mercedis*. When outflows were high, water levels in the marsh were high and showed little tidal fluctuation. Therefore trawling was less efficient because there was more water and more flooded vegetation available as cover for fish. However, even under these conditions most of the sampling areas were rarely more than 2 m deep, so our trawl covered at least half the water column, and large catches were common, especially early in the study. Therefore, variation in sampling efficiency may have exaggerated the peaks and valleys of the catch curves (Figs. 4, 5) but was unlikely to obscure the general trends in abundance. Probably the most important contributor to the seasonal patterns was the increase in young-of-year striped bass, splittail, prickly sculpin, and tule perch, in June through August. These species (and others, to a lesser extent) became vulnerable to our trawl at 30-40 mm SL, and catches of several hundred individuals in a 5-min tow were made on occasion. The rapid growth of these species during summer (Daniels and Moyle 1983; Herbold and Moyle, unpubl. data) indicated that environmental conditions, including warm temperatures and moderate salinities, were favorable for them and for other euryhaline species (e.g., staghorn sculpin, starry flounder). These same conditions also favored *N. mercedis*, a small shrimp that is an important food item in summer diets of most of the fishes (Herbold fn. 4). It is possible that the summer peak in fish abundance may be due also in part to fishes moving in to take advantage of an abundant food resource. The decline in *N. mercedis* abundance in late summer may be related in part to fish predation, although it is presumably related mainly to their seasonal movements within the entire estuary (Orsi and Knutson 1979).

The overall decline in fish abundance over the study period seemed to be due to two factors: variation in reproductive success of major species and the fact that 1982 and 1983 were years of unusually high precipitation and runoff, so freshwater conditions prevailed throughout the summer months of both years. Splittail showed an unusually strong year class in 1978, which dominated the 1979, and, to a lesser extent, 1980 samples (Daniels and Moyle 1983). Catches of splittail in 1979 were typically 2-5 times greater than in subsequent years. Striped bass, tule perch, and carp also showed peaks of abundance in 1979 and had low abundances in 1982-83, with one or two peaks of abundance in between. Except for carp, the peaks were largely due to influxes of young-of-year fish. The reason for the abundance of the 1978 year class of fish was presumably related to 1978 being a year of high, but not excessive, outflows. Increased reproductive success during high outflow years has been documented for striped bass (Stevens 1977), splittail (Daniels and Moyle 1983), American shad, chinook salmon, and longfin smelt (Stevens and Miller 1983). However, under extreme outflow conditions (such as existed in 1982 and 1983), young-of-year fish are apparently carried downstream to areas below the marsh (San Francisco and San Pablo Bay) where chances of survival may be less (Stevens 1977).

Drought also contributed to the variation in the fish fauna. During 1976 and 1977, severe drought reduced freshwater inflows to the marsh, resulting in sustained high salinities. Freshwater fishes declined dramatically during the drought period (Herrgesell et al. 1981) and the fishery for catfish (mainly white catfish and black bullhead) was greatly reduced (Baracco 1980). The catfish populations did not recover during the study period, but the regular appearance of young-of-year white catfish in our trawls in late 1983 indicated a recovery may be in progress. Other freshwater fishes found in the marsh (Table 1) showed no signs of increasing. Most were represented in our samples by <10 individuals that

had presumably been washed into the marsh from freshwater habitats upstream. However, black crappie and perhaps other centrarchids contributed to the local fishery prior to the drought, mainly in the upper ends of the larger sloughs, so a recovery can be expected.

Despite the decline in freshwater fishes during the drought, there was no corresponding major increase in the abundance of euryhaline marine species characteristic of nearby San Francisco Bay (Herrgesell et al. 1981). Marine species (such as northern anchovy, Pacific herring, and shiner perch) generally appeared in our samples in late summer when salinities were highest, in parts of the marsh closest to Suisun Bay.

Considering the annual and long-term variations in fish abundances and the fact that the fish assemblage is made up of a mixture of native and introduced species, the consistency of the assemblage structure during the study is surprising. Coevolution has obviously little role in an assemblage in which the most abundant species (striped bass) entered in 1879 and other abundant species entered in the 1960's (yellowfin goby) and 1970's (inland silversides) (Moyle 1976). The apparent consistency in structure seemed to be the result of 1) two introduced species, striped bass and carp, that were consistently abundant in the marsh, 2) the group of native resident fishes that was persistent in deadend sloughs, and 3) the native fishes that moved in and out of the marsh on a seasonal basis.

This does not mean that the structure observed during this study will persist indefinitely. A number of changes in the fish fauna may already be occurring. For example, the presence of young-of-year white catfish in 1983 and 1984 may signify a shift of the assemblage towards catfishes and centrarchids, such as existed before the 1976-77 drought. Striped bass are presently in a long-term decline in abundance, a trend which seems to be continuing (Kelley et al. 1982). Past history indicates that new introductions of fishes into the system are likely: specifically, the white bass, *Morone chrysops*, has recently become established in part of the San Joaquin drainage and may become a major new predator in the Sacramento-San Joaquin Estuary if planned eradication attempts fail (California Department of Fish and Game unpubl. data). Furthermore, additional diversions of freshwater from the estuary are planned (Herrgesell et al. 1981), and major modifications to the marsh channels are planned or underway (Baracco 1980), so the environment, especially in the dead-end sloughs, may change significantly. It is difficult to predict what the combined effects of all these changes will be on the present fish assemblage, but extinctions of both native and introduced species in the estuary have occurred in the past (Moyle 1976) and could occur again in the future.

The structure of the fish assemblage of Suisun Marsh is similar in may respects to the structure of the fish assemblages of other large estuaries (e.g., Markle 1976; Meeter et al. 1979), despite the importance of recently introduced species and the stabilizing influence humanity has had on the pattern and amount of freshwater inflow (Kahrl 1978). In most such estuaries, as in the Sacramento-San Joaquin, the assemblages are dominated by juvenile fishes, and most species have substantial populations outside the estuary. As in Suisun Marsh, the fish assemblages of such estuaries are made up of a relatively small number of the species available in nearby marine and freshwater environments. Presumably, the species composition of an estuarine assemblage is determined in large part by the ability of the species to tolerate the particular set of environmental conditions that exist there. Since these conditions may change with short-term climatological changes, the fish assemblages may change as well (Meeter et al. 1979; Marais 1982). Thus coevolution is given little chance to operate in estuarine systems in general. In this context, it is not surprising that the fish assemblage of the Suisun Marsh behaves ecologically in a way similar to fish assemblages in most other estuarine systems. Because resource partitioning is commonly observed among estuarine fishes (Sheridan and Livingston 1979; Whitfield 1980), competition may be an important process in determining the structure of estuarine fish assemblages (Thorman 1982), a hypothesis we are currently investigating in the Suisun Marsh.

ACKNOWLEDGMENTS

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LITERATURE CITED

ALLEN, L. G.
1982. Seasonal abundance, composition, and productivity of the littoral fish assemblage in Upper Newport Bay, California. Fish. Bull., U.S. 80:769-790.

BALTZ, D. M., AND P. B. MOYLE.
1982. Life history characteristics of tule perch (*Hysterocarpus traski*) populations in contrasting environments. Environ. Biol. Fishes 7:229-242.

BARACCO, A.
1980. Aquatic resources of Suisun Marsh with an analysis of the fishery effects of a proposed water quality maintenance plan. Calif. Dep. Fish Game, Anad. Fish. Branch Admin. Rep., 26 p.

BLABER, S. J. M., AND T. G. BLABER.
1980. Factors affecting the distribution of juvenile estuarine and inshore fish. J. Fish. Biol. 17:143-162.

CONOMOS, T. J. (editor).
1979. San Francisco Bay: the urbanized estuary. Pac. Div. AAAS, San Franc., 493 p.

DAHLBERG, M. D., AND E. P. ODUM.
1970. Annual cycles of species occurrence, abundance, and diversity in Georgia estuarine fish populations. Am. Midl. Nat. 83:382-392.

DANIELS, R. A., AND P. B. MOYLE.
1983. Life history of the splittail, (Cyprinidae: *Pogonichthys macrolepidotus*), in the Sacramento-San Joaquin estuary. Fish. Bull., U.S. 81:647-654.

DIXON, W. J., AND M. B. BROWN (EDITORS).
1977. Biomedical computer programs, P-series. Univ. Calif. Press, Berkeley, 880 p.

GANSSLE, D.
1966. Fishes and decapods of San Pablo and Suisun Bay. *In* D. W. Kelley (editor), Ecological studies of the Sacramento-San Joaquin estuary, Part I. Zooplankton, zoobenthos, and fishes of San Pablo and Suisun Bays, Zooplankton and zoobenthos of the Delta, p. 64-94. Calif. Dep. Fish. Game, Fish Bull. 133.

HERRGESELL, P. L., D. W. KOHLHORST, L. W. MILLER, AND D. S. STEVENS.
1981. Effects of freshwater flow on fishery resources in the Sacramento-San Joaquin estuary. *In* R. D. Cross and D. L. Williams (editors), Proceedings of National Symposium on Freshwater Inflow to Estuaries, p. 71-87. U.S. Fish and Wildlife Service OBS 81-4.

KAHRL, W. J. (EDITOR).
1978. The California water atlas. Calif. Dep. Water Resour., 118 p.

KELLEY, D. W., AND THE STRIPED BASS WORKING GROUP.
1982. The striped bass decline in the San Francisco Bay-Delta Estuary. Calif. State Water Res. Control Board, 58 p.

KJELSON, M. A., AND D. R. COLBY.
1977. The evaluation and use of gear efficiencies in the estimation of estuarine fish abundance. *In* V. F. Kennedy (editor), Estuarine processes, Vol. 2, p. 416-424. Academic Press, N.Y.

LIVINGSTON, R. J.
1976. Diurnal and seasonal fluctuations of organisms in a North Florida estuary. Estuarine Coastal Mar. Sci. 4:373-400.

MARAIS, J. F. K.
1982. The effects of river flooding on the fish populations of two eastern Cape estuaries. S. Afr. J. Zool. 17:96-104.

MARKLE, D. F.
1976. The seasonality of availability and movements of fishes in the channel of the York River, Virginia. Chesapeake Sci. 17:50-55.

MEETER, D. A., R. J. LIVINGSTON, AND G. C. WOODSUM.
1979. Long-term climatological cycles and population changes in a river-dominated estuarine system. *In* R. J. Livingston (editor), Ecological processes in coastal and marine systems, p. 315-338. Plenum Press, N.Y.

MOYLE, P. B.
1976. Inland fishes of California. Univ. Calif. Press, Berkeley, 405 p.

ORSI, J. J., AND A. C. KNUTSON, JR.
1979. The role of mysid shrimp in the Sacramento-San Joaquin estuary and factors affecting their abundance and distribution. *In* T. J. Conomos (editor), San Francisco Bay: the urbanized estuary, p. 401-408. Pac. Div. AAAS, San Franc.

QUINN, N. J.
1980. Analysis of temporal changes in fish assemblages in Serpentine Creek, Queensland. Environ. Biol. Fishes 5:117-133.

SHERIDAN, P. F., AND R. J. LIVINGSTON.
1979. Cyclic trophic relationships of fishes in an unpolluted, river-dominated estuary in North Florida. *In* R. J. Livingston (editor), Ecological processes in coastal and marine systems, p. 143-160. Plenum Press, N.Y.

SIEGFRIED, C. A.
1980. Seasonal abundance and distribution of *Crangon franciscorum* and *Palaemon macroadactylus* (Decapoda, Caridea) in the San Francisco Bay-Delta. Biol. Bull. (Woods Hole) 159:177-192.

SKINNER, J. E.
1972. Ecological studies of the Sacramento-San Joaquin Estuary. Calif. Dep. Fish, Game Delta Fish Wildl. Prot. Study Rep. 8, 94 p.

SMITH, J. J.
1982. Fishes of the Pajaro River System. Univ. Calif. Publ. Zool. 115:83-170.

STEVENS, D. E.
1977. Striped bass (*Morone saxatilis*) year class strength in relation to river flow in the Sacramento-San Joaquin Estuary, California. Trans. Am. Fish. Soc. 106:34-42.

STEVENS, D. E., AND L. W. MILLER.
1983. Effects of river flow on abundance of young chinook salmon, American shad, longfin smelt, and delta smelt in the Sacramento-San Joaquin River system. N. Am. J. Fish. Manage. 3:425-437.

THORMAN, S.
1982. Niche dynamics and resource partioning in a fish guild inhabiting a shallow estuary on the Swedish west coast. Oikos 39:32-39.

TURNER, J. L., AND D. W. KELLEY (EDITORS).
1966. Ecological studies of the Sacramento-San Joaquin Delta. Part II. Fishes of the Delta. Calif. Dep. Fish Game, Fish Bull. 136, 168 p.

WHITFIELD, A. K.
1980. Distribution of fishes in the Mhlanga estuary in relation to food resources. S. Afr. J. Zool. 15:159-165.

THE ROLE OF ESTUARINE AND OFFSHORE NURSERY AREAS FOR YOUNG ENGLISH SOLE, *PAROPHRYS VETULUS* GIRARD, OF OREGON

E. E. KRYGIER[1] AND W. G. PEARCY[2]

ABSTRACT

Our trawling studies confirm that age group 0 English sole are common in shallow waters along the open coast as well as in estuaries of Oregon. Both areas appear to be important nursery areas for this species. Metamorphosing English sole were recruited to Yaquina Bay over many months between November and June during the 5 years studied. Seasonal trends in abundance of these transforming fish were rather similar to both Yaquina Bay and open coastal stations. Transforming individuals, however, were found earlier in the fall and later in the spring and summer along the open coast than in Yaquina Bay.

Based on catch curves, the densities (no. m^{-2}) of juvenile English sole were much higher in Yaquina Bay than along the open coast. Transforming sole (20-25 mm) were an exception. They were sometimes most abundant at the open coast location. Increasing densities of 20-40 mm length fish in the Yaquina Bay catches were accompanied by decreased catches of this size group at the open coast site. This suggests immigration of a broad size range of both transforming and fully transformed individuals into Yaquina Bay.

English sole, *Parophrys vetulus* Girard 1854, is a major component of the catches in the northeastern Pacific trawl fishery, usually ranking second only to Dover sole, *Microstomus pacificus*, in annual landings off Oregon (Barss 1976[3]; Demory et al. 1976[4]). It ranges from Baja California to Unimak Island in western Alaska, with commercial quantities at depths of 128 m or less (Hart 1973). Tagging studies have revealed a series of relatively discrete stocks of English sole off California, Oregon, Washington, and British Columbia (Ketchen 1956; Forrester 1969; Jow 1969; Pattie 1969; Barss 1976 fn. 3).

Spawning of English sole is protracted, usually extending from September through April, and is often variable in seasonal intensity within and among spawning seasons (Budd 1940; Ketchen 1956; Harry 1959; Jow 1969; Laroche and Richardson 1979). Much of this variability among years may be related to upwelling and bottom temperatures (Kruse and Tyler 1983). Spawning concentrations of adult English sole were found in the fall off the central Oregon coast at depths of 70-110 m (Hewitt 1980).

English sole are fecund, producing 327,600-2,100,000 eggs, depending on the size of female (Ketchen 1947; Harry 1959). Eggs are pelagic and hatch in about 4½ d at 10°C (Alderdice and Forrester 1968). Larvae are often abundant during late winter and early spring in coastal waters of Oregon (Richardson and Pearcy 1977; Mundy 1984). Larval abundance may fluctuate greatly among years, possibly due to annual differences in ocean conditions (Laroche and Richardson 1979; Mundy 1984). The pelagic phase lasts 8-10 wk (Ketchen 1956; Laroche et al. 1982), and most individuals complete metamorphosis and acquire the morphology of benthic pleuronectids at 20 mm SL and 120 d of age (Ahlstrom and Moser 1975; Rosenberg and Laroche 1982).

While early larval stages are rarely found in estuaries (Misitano 1970; Pearcy and Myers 1974), transforming larvae and early juvenile stages of English sole are common in estuaries (Westrheim 1955; Smith and Nitsos 1969; Olsen and Pratt 1973; Pearcy and Myers 1974; Misitano 1976; Toole 1980; Bayer 1981) and shallow protected bays (Ketchen 1956; Kendall 1966; Van Cleve and El-Sayed 1969). Young English sole are known to utilize 13 estuaries along the Oregon coast and were absent in only 3 small estuaries surveyed along the southern Oregon coast.[5] Villadolid (1927, as cited by Misitano 1970) captured

[1]College of Oceanography, Oregon State University, Corvallis, OR; present address: Alaska Trollers Association, 130 Seward Street, Juneau, AK 99801.

[2]College of Oceanography, Oregon State University, Corvallis, OR 97731.

[3]Barss, W. H. 1976. The English sole. Oreg. Dep. Fish Wildl., Inf. Rep. 76-1, 7 p.

[4]Demory, R. L., M. J. Hosie, N. Ten Eyck, and B. O. Forsberg. 1976. Marine resource surveys on the continental shelf off Oregon, 1971-74. Oreg. Dep. Fish Wildl., 49 p.

[5]Report of estuary surveys, July-August 1972. Fish Comm. Oreg. Intern. Rep. GS-73-1, 14 p.

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0-age English sole in San Francisco Bay but not off the coast.

Based on the incidence of a parasitic infection, apparently acquired only in estuaries, and the absence of 0-age English sole in Demory's (1971) surveys off the northern Oregon-southern Washington coast, Olsen and Pratt (1973) concluded that estuaries are likely the exclusive nursery for English sole on the Oregon coast. Laroche and Holton (1979), however, captured 0-age English sole in shallow waters along the open Oregon coast, indicating that estuaries may not be the only nursery area for English sole off Oregon.

The main objective of our study is to evaluate the relative importance of estuarine and open coastal nursery grounds for young English sole off Oregon.

METHODS AND MATERIALS

Bottom trawl collections provided most of the information on the distribution and abundance of juvenile English sole. Collections were made in Yaquina Bay and along the open coast outside the bay. These were supplemented with extensive trawl collections farther to the north and south along the open coast and collections in other estuaries.

Fish were collected using a 1.52 m wide, 56 cm high beam trawl (see Krygier and Horton 1975) from the RV *Paiute* and from a 7.3 m dory. Additional collections with a 2.72 m beam trawl (Carey and Heyamoto 1972) were made on the RV *Cayuse*. To retain small, settling fish, fine-mesh (1.5-3.5 mm stretch) liners were used in the trawls. The 1.52 and 2.72 m beam trawls were fitted with a 1.0 or 2.0 m circumference wheel, respectively, and a revolution counter to estimate the area sampled (Carey and Heyamoto 1972; Krygier and Horton 1975). Tows were made at 0.7-1.0 m s^{-1}. Tow duration was normally 5-10 min on the bottom in estuaries and 10-20 min along the coast, usually at a 4:1 scope. Most tows were during daylight hours.

Collections for juvenile English sole were made in five different study areas (Fig. 1, Table 1):

ESTUARINE

1) Yaquina Bay: 1.52 beam trawl collections were made in lower Yaquina Bay from January 1970 through February 1972 by Krygier and Johnson (unpubl. data) and Krygier and Horton (1975) and supplemented by collections in 1977-79. Additionally, we used collections made by Myers (1980) with a 100 m beach seine (11.0 mm stretch mesh in the inner wing and bunt (Sims and Johnsen 1974)).

2) Other estuaries: The 1.52 m beam trawl was towed from a 7.3 m dory in four estuaries north and south of Yaquina Bay (Tillamook and Siletz Bays, 107.5 and 35.2 km to the north of Yaquina Bay and Alsea Bay and Umpqua River estuary, 21.3 and 105.6 km to the south). Each estuary was divided into seven equal-area portions from which we planned to take three random trawl collections (2 of the 21 trawls in the Umpqua River estuary were not completed).

COASTAL

3) Moolack Beach: 1.52 m beam trawl collections were made on a monthly or bimonthly basis in shallow (3-31 m depth) nearshore waters in a 1.0 km^2 area just north of Yaquina Head during 1977, 1978, and 1979. Moolack Beach is semiprotected by headlands to the north and south and offshore by a reef that rises from 15 m to 6 m.

4) Grid stations: Collections were taken with a 2.72 m beam trawl, approximately monthly, during 1978 at 1.9, 5.6, and 9.3 km (1, 3, and 5 nmi) offshore along lat. 44°41.6′N, 44°36.6′N, and 44°31.6′N. Thirteen collections were also made in this area with the 1.52 m beam trawl.

TABLE 1.—Summary of collections used in this study.

Area	Net type	No. trawls	Dates (sampling frequency)
Yaquina Bay	[1]1.52 m	178	16 Jan. 70-25 Jan. 71 (weekly or biweekly); 17 Feb. 71-25 Feb. 72 (bimonthly)
	[2]1.52 m	26	26 Apr.-28 June 77 (bimonthly)
	[2]1.52 m	96	1 Dec. 77-14 Sept. 79 (monthly to bimonthly)
	[2]2.72 m	8	16 Nov. 77, 1 Feb. 78, 27 Nov. 78
	beach seine	196	12 July 77-11 Nov. 78 (various: daily, biweekly, weekly, bimonthly)
Moolack	1.52 m	16	28 Apr. 77-23 June 77 (bimonthly)
	1.52 m	76	11 Jan. 78-24 Sept. 79 (bimonthly of monthly)
Grid	1.52 m	13	21 Apr. 77-27 June 77; 15 June 78-28 Sept. 78
	2.72 m	106	17 Nov. 77-25 Oct. 78 (monthly)
North-South	1.52 m	40	2 June 77-13 June 77, 15 June 78-21 July 78
	2.72 m	83	15 May 78, 27 June 78, 25 Oct. 78
Estuaries	1.52 m	82	8-12 May 78, 21 trawls each in Tillamook, Siletz and Alsea; 19 trawls in Umpqua

[1]Net liners 3.5 mm and cod end liner of 1.5 mm stretch mesh, 1970-72.
[2]Net liners 3.2 mm stretch mesh, 1977-79.

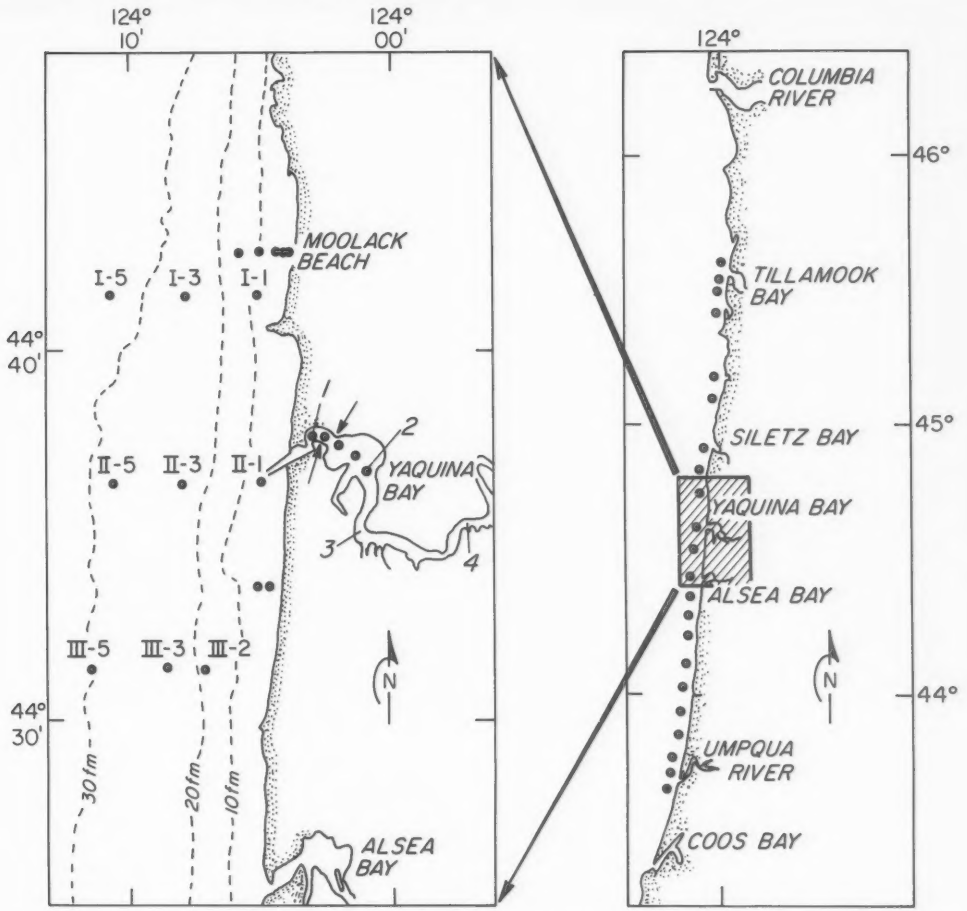


FIGURE 1.—Location of sampling stations in the North-South coastal survey (right) and at Moolack Beach, the grid stations I, II, III, and within Yaquina Bay (left). In Yaquina Bay the numbers 1-4 indicate locations of stations for sampling in 1970-72, the solid dots locations in 1977-79, and the arrows indicate seine stations in 1977.

5) North-south coastal survey: 1.52 m beam trawl collections were made from 111 km to the north (lat. 45°37.5'N) and 111 km to the south (lat. 45°36'N) of Yaquina Bay at 9.3 km intervals (Fig. 1) at depths of 9-18 m in June 1977 and May-October 1978.

Most samples were preserved in 5% Formalin[6] and seawater. In the laboratory, fish were identified, sorted, and standard length (SL) measured to the nearest millimeter. Nearly all English sole captured in Yaquina Bay were 150 mm SL or less and included 0- and I-age fish (Rosenberg 1982). We call these fishes "juveniles" in this paper.

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Variability of Catches

The variability of the number of juvenile English sole caught per m^2 in repeated trawls within the same area was low. Coefficients of dispersion ($s^2/\bar{x}$)

were usually <0.1, indicating uniform distributions within the small areas (10-100 m^2) and short intervals of time (1-2 h) sampled. Variability was higher and coefficients of dispersion sometimes differed significantly (chi-square, <0.05) from a random (Poisson) distribution among different sampling depths at the same date ($s^2/\bar{x}$ = 0.36-1.65) and among different sampling dates within a single depth at Moolack Beach ($s^2/\bar{x}$ = 1.2-2.31). Coefficients of dispersion did not significantly differ from randomness either among the grid stations for the same sampling dates ($s^2/\bar{x}$ = 0.87-1.82) or among different sampling dates at the same station (0.94-1.97). In general, at the scale of sampling we used, juvenile English sole had even, nonpatchy distributions.

Gear Comparisons

To compare the relative efficiencies of the 1.52 m beam trawl from the *Paiute* and the 2.72 m beam trawl from the *Cayuse*, 14 pairs of trials were made at the same time, while the vessels trawled on parallel courses within 30 m of each other. No significant differences ($P > 0.05$; Mann-Whitney "U" tests, Tate and Clelland 1957) were found in the catch/m^2 of juvenile English sole <150 mm for any paired trawl comparison.

No significant differences were found in length-frequency distributions of *P. vetulus* captured in 10 of the 14 comparisons [Kolmogorov-Smirnov (K-S) test, Tate and Clelland 1957]. In the four pairs of tows that were significantly different (October 1978) the 2.72 m trawl caught more small (~20 mm SL) English sole per m^2 than the 1.52 m trawl, while both trawls caught similar proportions in the 46-100 mm size range.

Comparisons were made between the sizes of English sole in beach seine samples and midchannel trawl samples in Yaquina Bay on six different dates. Differences were significant (K-S test; $P < 0.05$) for all comparisons because the beam trawl caught a much broader size range of fish, including individuals >40 mm which were rare or absent in the beach seine catches.

Trends in Catches and Sizes of Fish

Significant (H-test, $P \leq 0.05$) differences in catches/m^2 at different depths at Moolack Beach and the grid stations show that in general the abundance of juvenile English sole in offshore waters was greatest in shallow water and decreased with increasing depth. Average catches/$10^3 m^2$ (±1 standard deviation) of English sole ≤150 mm were 16 (±20), 61 (±14), 43 (±75), and 10 (±12) at the 9, 9-17, 12-18, and 18-31 m stations off Moolack Beach, compared with only 3 (±3) and 2 (±3) at the 40 and 64 m I-3 and I-5 grid stations at about the same latitude.

Newly transformed, benthic English sole (<24 mm) were found at all depths sampled in the Moolack Beach area, but the highest proportion of these recently metamorphosed fish was found at depths <18 m. Within the depth zones sampled the proportion of small English sole <30 mm decreased with depth and fish >150 mm were only captured at depths deeper than 18 m (Fig. 2).

Juvenile English sole ≤150 mm were found along the entire 222 km coast sampled (Fig. 3). They were usually moderately abundant (≥0.01 m^2) between Siletz Bay and Alsea Bay, and near the Umpqua River and Tillamook Bay. Average catches, however, were higher off Moolack Beach than any other area, averaging 0.21 juvenile English sole/m^2, an order of magnitude greater than most other offshore areas or the grid stations. Moolack Beach was apparently a region of the open coast with exceptionally high densities of English sole.

Juvenile English sole were generally most abundant at the shallowest depths in these collections, corroborating more intense sampling off Moolack Beach and at the grid stations (Fig. 3). Average catches at depths of 18 m and 36 m decreased about an order of magnitude between May (0.026/m^2; SD 0.049) and October (0.003/m^2; SD 0.003).

Variations in Abundance of Settling Fish

In our samples, metamorphosis or transformation, as indicated by migration of the left eye and by body pigmentation, occurred between 14-26 mm. Most fish had completed metamorphosis by 23 mm. In Yaquina Bay, the metamorphosing individuals first appeared in November of 1971 and 1978 (the 1972 and 1979 year classes) and in January of 1971 and 1978 (1971 and 1978 year classes) (Fig. 4). (In this paper we designate year classes by the year that most juveniles settled to the bottom; e.g., products of spawning during the fall 1978-winter 1979 are called the 1979 year class.) Metamorphosing fish were present in Yaquina Bay until June (1970, 1978, 1979) or July (1971), but none was found after July during the four summer periods sampled.

Maximum densities of these metamorphosing fish were observed between March and May in 1970, 1971, and 1978, but between November and January in 1978-79. Densities were variable. Low densities

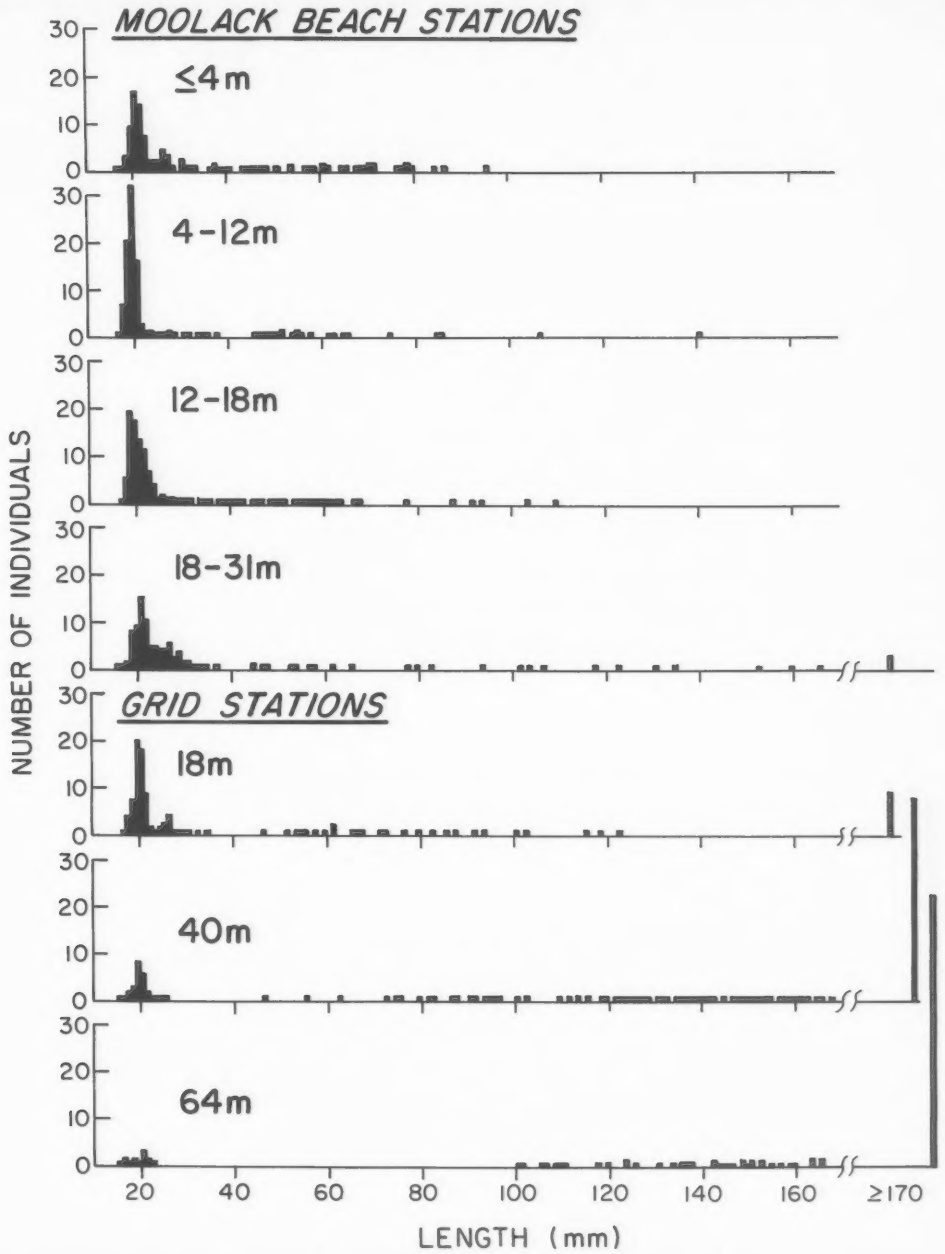


FIGURE 2.—Length-frequency distributions of juvenile English sole caught at different depths at the Moolack Beach (above) and grid stations (below).

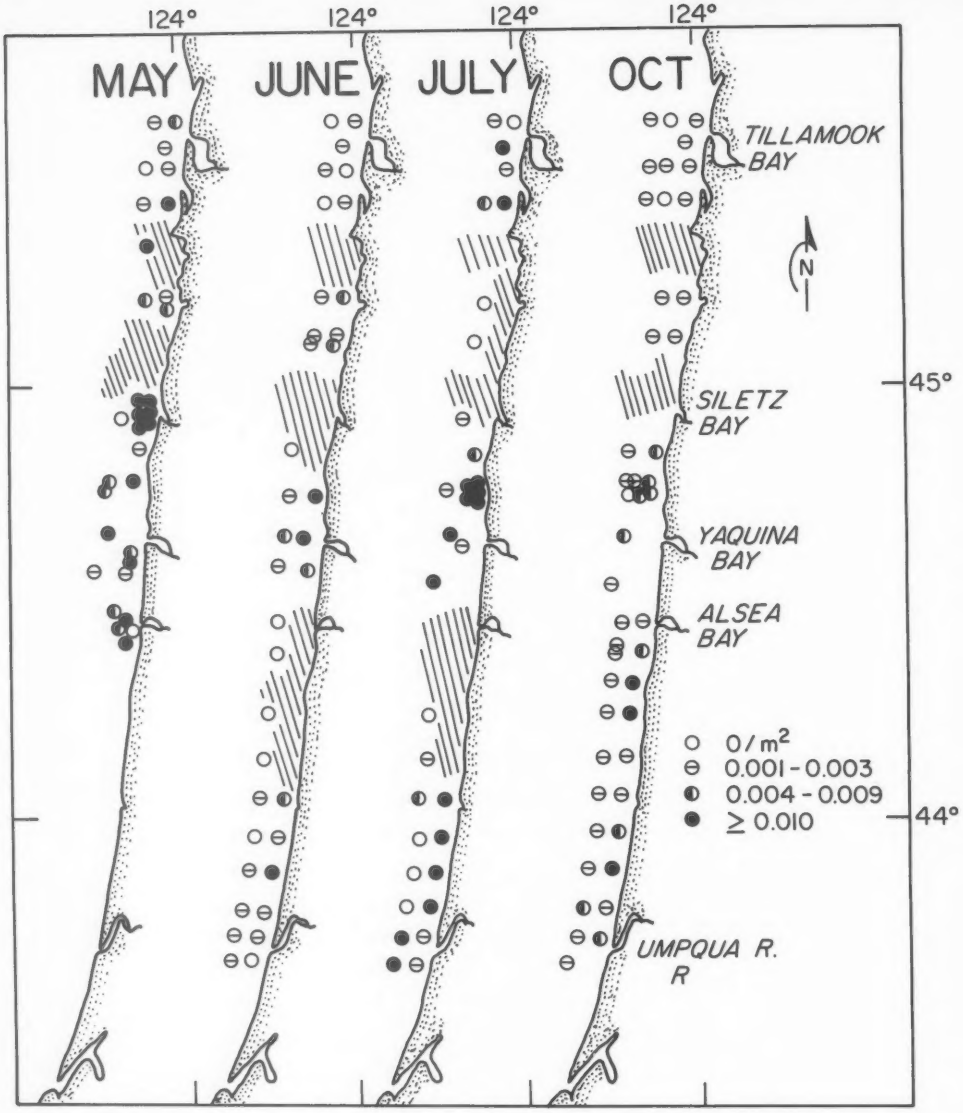


FIGURE 3.—Catches of juvenile English sole (<150 mm) along the open coast during May, June, July, and October 1978. Hatched areas indicate untrawlable grounds due to crab pots or rocky outcrops.

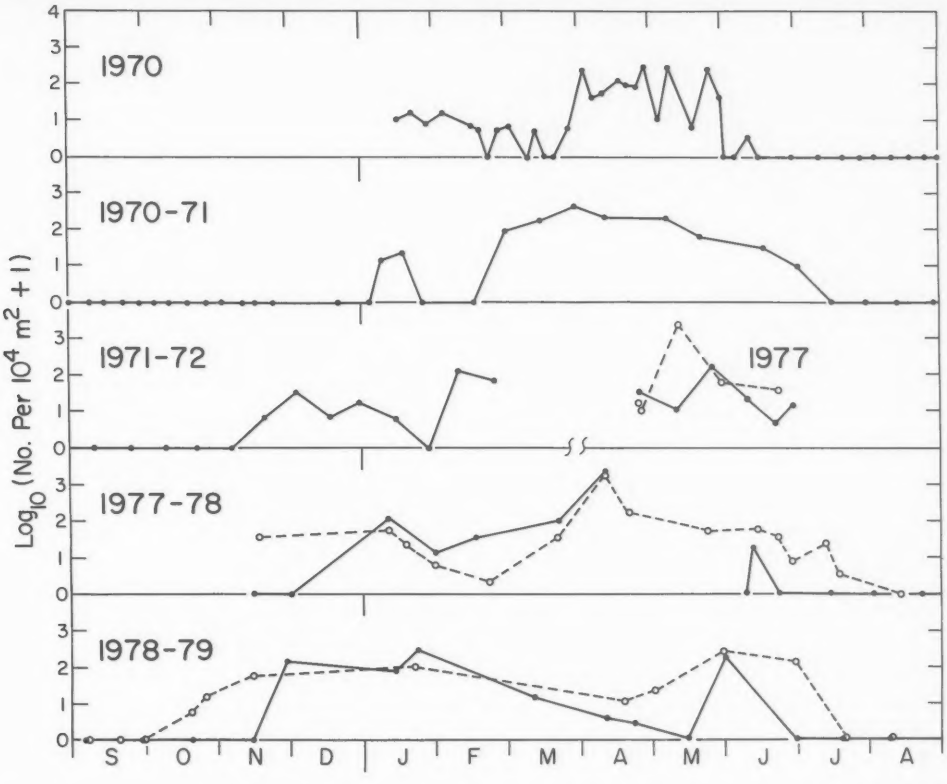


FIGURE 4.—Abundances of settling (<20 mm SL) English sole in Yaquina Bay for 1970-79 (solid line) and Moolack Beach for 1970-79 (dashed line).

occurred during March 1970, January and February 1971, 1972, and April-May 1979, suggesting seasonal variation in spawning activity of adults (see Kruse and Tyler 1983), mortality of planktonic stages, or movement of young into or out of the estuary.

Seasonal trends in catches of transforming English sole in Yaquina Bay and at Moolack Beach for 1978 and 1979 shows that fish ≤20 mm were found 1-2 mo earlier at Moolack Beach than in Yaquina Bay during both years (Fig. 4). Moreover, recruitment of the 1978 and 1979 year classes continued at Moolack Beach from 18 to 50 d after settling fish were no longer found within the estuary. To our surprise, similar densities of settling fish were caught in both areas. Seasonal trends were sometimes similar, suggesting a common source of larvae and similar processes affecting variations in recruitment of metamorphosing fish at both the open-coast and estuarine areas.

The catches/m^2 of age groups 0 and I English sole (20-150 mm) are plotted as catch curves for each 5 mm size group (Fig. 5) where

$$\text{no. } m^2 = \frac{\Sigma \text{ of the number of individuals in each 5 mm size group}}{\text{total area sampled in } m^2 \text{ during sampling periods in which year class occurred}}$$

Trends in the abundance of English sole were often

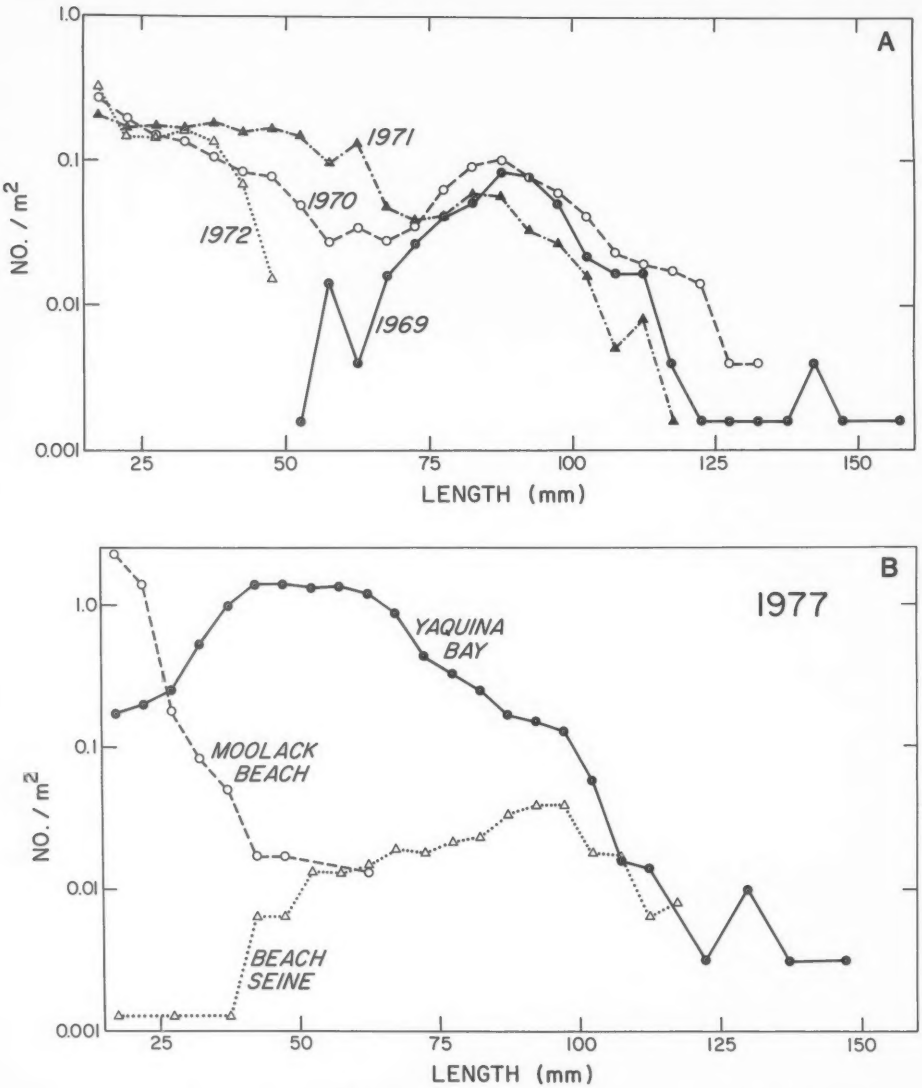
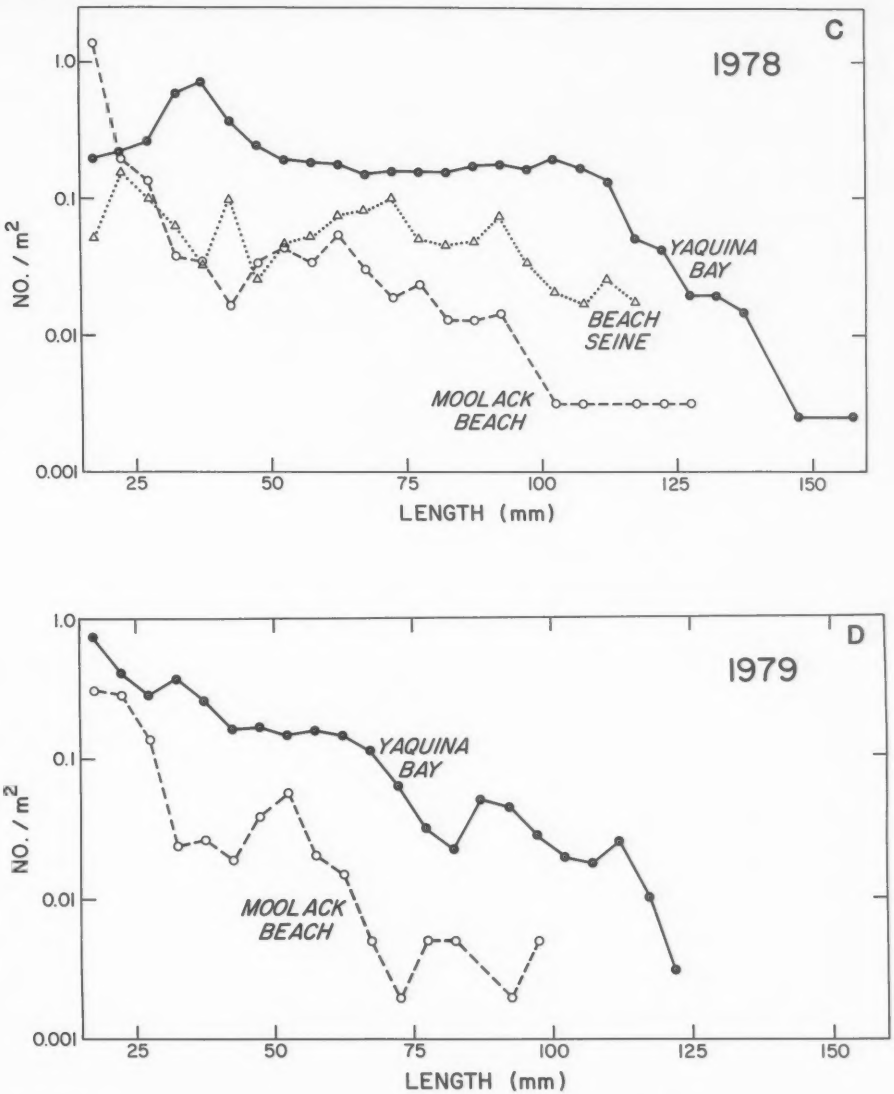


FIGURE 5.—Abundances of young English sole year classes as a function of length. (A) 1969-72, (B) 1977,

similar for the four year classes sampled between 1969 and 1972 in Yaquina Bay (Fig. 5A). Abundances of recently recruited individuals 20-45 mm in length were similar among the 1970, 1971, and 1972 year classes. The 1969, 1970, and 1971 year classes also increased in numbers/m^2 between 75 and 90 mm before declining to low catches at larger sizes. Abundances of small fish of the 1969 year class are low because this year class was only sampled in 1970, when most fish were >75 mm.

Catches/m^2 of the 1977 and 1978 year classes in Yaquina Bay were generally larger than the 1969, 1970, 1971, 1972, and 1979 year classes (Fig. 5A, B, C). The 1977 cohort differed from other year



(C) 1978, (D) 1979 year classes. Note that some curves are based on incomplete sampling of all seasons.

classes by having a large peak of abundance for 30-70 mm individuals, and the 1978 year class had much higher abundance of large (100-140 mm) individuals than other year classes.

Obviously the trends shown by these catch curves cannot be explained by mortality alone. Immigration of young benthic English sole into our sampling area of Yaquina Bay is suggested by the increased catches of 75-100 mm individuals of the 1970 and 1971 year classes and increased catches of 20 to 40-45 mm individuals of the 1978 and 1979 year classes.

Beam trawls catches at Moolack Beach for the 1977, 1978, and 1979 year classes and beach seine catches in Yaquina Bay for part of the 1977 year class

and the 1978 year class indicate that the abundance of newly recruited, settling fish (<24 mm) of the 1977 and 1978 year classes was higher at Moolack Beach than in Yaquina Bay (Fig. 5B, C). These high catches at Moolack Beach were followed by a steep decline in catches to the 41-44 mm size class. English sole larger than 30 mm were consistently less abundant at Moolack Beach than in Yaquina Bay. Densities increased in Yaquina Bay concurrent with the steep decline of 20-44 mm individuals at Moolack Beach. These trends suggest immigration of young fish from the shallow waters of the open coast to Yaquina Bay over a range of sizes, from 20 to 40 mm.

Two peaks occurred in the beach seine catches of the 1978 year class: at 20-25 and 40-45 mm. The first peak coincides with the sizes that decreased markedly in abundance at Moolack Beach. The second peak coincides with low abundance of 40-45 mm fish at Moolack, and with a decrease in catches of these sizes of fish at the trawl stations in Yaquina Bay. These trends of trawl-caught fish suggest that immigration from Moolack Beach first occurred to the shallow waters of the bay and then to the deeper trawl stations. The peak in the catches of 40-45 mm fish at seine stations may be caused by immigration into these shallower waters of metamorphosed individuals from either the offshore areas or deep areas of Yaquina Bay.

Abundances and Sizes in Five Estuaries

Age-0 English sole were present in all five estuaries sampled with trawls during May and June 1978. The mean abundance of young English sole, which ranged from 0.7/m^2 in Tillamook Bay to 0.02/m^2 in the Umpqua estuary, generally decreased from the northern to the southern estuaries (Table 2). The exception was Yaquina Bay. It was latitudinally the middle estuary, yet abundance of English sole there ranked above that in Siletz Bay. No consistent relationship was observed between mean abundances and the area of estuaries, river flows, tidal prisms, or flushing times using the data of Choi (1975) or Starr (1979)[7].

A broad size range of fish was caught in Tillamook, Siletz, and Alsea Bays, while we caught few individuals larger than 36 mm in the Umpqua River estuary (Table 3). In Yaquina Bay, a higher proportion of large individuals (>65 mm) was found than in the other estuaries. A much broader range of sizes was captured in these estuaries than in open coastal areas on the dates sampled.

TABLE 2.—Mean abundance and standard deviation of 0-age English sole in five estuaries north and south of Yaquina Bay and along the open coast between 9 and 37 m, April-June 1978.

Location	Date: 1978	No. of hauls	No./m^2	SD (s)
Estuary				
Tillamook Bay	8 May	21	0.715	0.916
Siletz Bay	9 May	21	0.184	0.206
Yaquina Bay	10 April; 12 July	6	0.332	0.251
Alsea Bay	10 May	21	0.059	0.075
Umpqua River estuary	12 May	19	0.016	0.037
Ocean Off				
Tillamook Bay	15 May; 17 June	12	0.005	0.013
Siletz Bay	16 May; 29 June	9	0.019	0.020
Alsea Bay	22, 29 June			
Umpqua River estuary	28 June	3	0.001	0.001
North of Newport	16, 23 May; 29 June	14	0.006	0.011
South of Newport	18 June	9	0.003	0.004

Growth

Despite prolonged recruitment of young English sole in Yaquina Bay (Fig. 4) distinct length modes were usually present for each sampling date. Growth rates in Yaquina Bay, estimated by following the progression of length modes of cohorts over time, were generally greatest (0.46-0.49 mm/d) during the late spring to early fall, while growth rates in winter were lower (0.26-0.32 mm/d) (Table 4). The growth rate from January to July 1970 was 0.47 mm/d, similar to the spring-fall estimates. Growth rates were estimated only for the spring-fall period off Moolack Beach. These were similar to those for Yaquina Bay fish but more variable, ranging from 0.28 to 0.42 mm/d.

DISCUSSION

Larvae of English sole are abundant in coastal waters off Oregon, ranking first among the flatfishes in some years (Richardson 1977[8]; Richardson and Pearcy 1977; Mundy 1984). Young larvae (<10 mm) of English sole are rare in estuaries of the Oregon-California coast as evidenced by plankton samples

[7]Starr, R. M. 1979. Natural resources of Siletz esturary. Oreg. Dep. Fish Wildl., Estuary Inventory Rep. 2(4):1-44.

[8]Richardson, S. L. 1977. Larval fishes in Ocean waters off Yaquina Bay, Oregon: Abundance, distribution and seasonality, January 1971 to August 1972. Oreg. State Univ. Sea Grant Publ. ORESU-T-77-003.

of only 6 larvae in 393 tows in Yaquina Bay (Pearcy and Myers 1974), 22 larvae in 84 tows in the lower Columbia River (Misitano 1977), and 4 larvae in 89 tows from Humboldt Bay (Eldridge 1970; Misitano 1970, 1976). However, young larvae are common in offshore collections (Porter 1964; Pearcy and Myers 1974; Laroche and Richardson 1979), and transforming larvae (19-22 mm) are frequent in collections from Humboldt Bay and the Columbia River estuary (Eldridge 1970; Misitano 1970, 1976). Thus young *P. vetulus* that enter estuarine nurseries do so as large transforming larvae or after completion of metamorphosis.

Our data confirm the above findings. We found that settlement of metamorphosing English sole to the bottom was common both in the Yaquina Bay estuary and at Moolack Beach along the open coast. Transforming individuals along the coast were caught in largest numbers/m^2 at depths of 16 m or less, but they were also captured at the deepest stations sampled (Fig. 2). Since small larvae were rare in Yaquina Bay (Pearcy and Myers 1974), these trends suggest movement into the bay of transforming larval stages. Boehlert and Mundy (in prep.)[9] have subsequently confirmed that small juveniles as well as transforming larvae of English sole recruit to Yaquina Bay.

Although densities of transforming larvae were sometimes higher at Moolack Beach than in Yaquina Bay, densities of juvenile fish >30 mm were usually over an order of magnitude higher in Yaquina Bay than at Moolack Beach, indicating either immigration into the bay from the open coast during or after metamorphosis, or dispersal or higher mortality rates of young along the open coast than in the estuary. Increasing densities in Yaquina Bay, concurrent with decreasing densities at Moolack Beach, suggest immigration into the bay over an extended range of sizes from 25 to 40 mm.

The mechanisms for such movements are not fully understood, but vertical movement of young fish off the bottom during periods of flood tide has been shown to effect transport into estuaries in several

TABLE 3.—Length distribution of English sole caught in the five estuaries, Moolack Beach and grid stations, 10 April-12 June 1978.

Location	No. of fish	Standard lengths (mm)														
		14-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-70	71-75	76-80	81-85	86-90
8:V:78																
Tillamook	2,979	904	1,619	296	48	19	23	26	31	13	4	4	2			
9:V:78																
Siletz Bay	673	242	256	72	36	13	13	21	14	5		1				
10:V:78																
Alsea Bay	306	41	98	49	25	20	15	19	27	9	1		1			1
12:V:78																
Umpqua River estuary	54	30	12	5	4			1						1	1	
10:IV:78																
Yaquina Bay	163	46	16	1	6	11	11	11	23	18	11	6	2	1		
12:VI:78																
Yaquina Bay	156	2	6	9	9	18	6	6	12	17	23	18	16	8	3	3
10:IV:78																
Moolack Beach	221	209	9	3												
12:VI:78																
Moolack Beach	24	5	12	5		1			1							
23:V:78																
Offshore grid	47	42	5													

TABLE 4.—Growth of juvenile English sole estimated from modal progression of size-frequency histograms from catches in Yaquina Bay and Moolack Beach, 1970-79.

Area and date	mm/d (slope)	r^2
Yaquina Bay		
Jan. 1970-July 1970	0.46	0.98
Dec. 1971-Feb. 1972	0.26	0.92
Jan. 1972-Feb. 1972	0.32	0.91
Jan. 1978-Apr. 1978	0.31	0.91
Apr. 1970-Oct. 1970	0.46	0.96
May 1971-Oct. 1971	0.47	0.98
Mar. 1979-Sept. 1979	0.49	0.96
Moolack Beach		
Aug. 1978-Oct. 1978	0.41	0.98
May 1978-Oct. 1978	0.28	0.93
Apr. 1979-Sept. 1979	0.38	0.96
May 1979-Aug. 1979	0.42	0.99
June 1979-Sept. 1979	0.36	1.00

[9]Boehlert, G. W., and B. C. Mundy. Recruitment dynamics of the English sole, *Parophrys vetulus*, to a west coast estuary. Unpubl. manuscr., 16 p. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, HI 96812.

flatfish species. Cruetzberg et al. (1978) suggested that immigration of plaice, *Pleuronectes platessa*, larvae is based on such a "selective tidal transport," and that starvation induces the swimming behavior resulting in transport by currents. De Veen (1978) concluded that juvenile sole (*Solea solea*) use tidal transport to enter the Wadden Sea in the spring. Metamorphosing larvae of the stone flounder, *Kareius bicoloratus*, also immigrate into estuarine nurseries with tidal currents; they were most abundant in plankton net collections during flood tides at night in an estuary of Sendai Bay, Japan (Tsurata 1978). Misitano (1976) captured metamorphosing English sole in a 1 m midwater trawl, especially after dark, in Humboldt Bay. Boehlert and Mundy (fn. 9) found that transforming English sole larvae were usually most abundant during flood tides at night in the moored plankton net that was nearest the bottom in the lower portion of the Yaquina Bay estuary and that recruitment to the bay was correlated with onshore Ekman transport.

Our estimates of growth from modal progressions length-frequency histograms [averaging 0.40 mm/d (s = 0.10) for Yaquina Bay and 0.37 mm/d (s = 0.06) for Moolack Beach] were considerably higher than Rosenberg's (1982) estimates even for the same years (Table 4). Rosenberg studied growth of 0-age English sole using fortnightly otolith rings as an aging technique. He calculated that fish, 140-480 d of age, collected during 1978 and 1979 in Yaquina Bay and at Moolack Beach grew about 0.28 mm SL/d. Estimates of growth rates of juvenile English sole from length data by Westrheim (1955) in Yaquina Bay, as well as by Smith and Nitsos (1969) in Monterey Bay, and Van Cleve and El-Sayed (1969) and Kendall (1966) in Puget Sound were more similar to our estimates than those of Rosenberg (1982, table 2). The differences in apparent growth rates between length frequency and otolith measurements are difficult to explain. Avoidance of nets by larger sole (e.g., Kuipers 1975), emigration of larger fish out of the sampling area in the late summer, and prolonged immigration of small fish into the estuary, are likely. Any of these would result in an underestimates of growth by the length-frequency method (see Rosenberg 1982 for opposite explanations). Differential mortality of small fish (Rosenberg 1982) or methodological difficulties in analyzing otolith growth increments may also help explain the differences.

Our study confirms the observations of Laroche and Holton (1979) that small 0-age English sole are not found exclusively in estuaries along the Oregon coast, and that average sizes of English sole increase with depth at Moolack Beach. Laroche and Holton (1979) suggested that even low density or localized utilization of the extensive unprotected offshore areas along the coast could be an important factor in determining the English sole production off Oregon. To evaluate this possibility, we determined total areas within the range of our sample depths in the lower reaches of the five estuaries and multiplied these areas by the average catch/m^2 of 0-age English sole (<90 mm) to obtain an estimate of total number of young English sole in each estuary. The average catch was also determined from 47 collections between 9 and 36 m where we found highest catches of 0-age fish, along 448 km of the open coast from our May-June catches (Table 2). The average catch/m^2 of 0-age sole in the five estuaries usually was many times that along the open coast. But because of the large differences in areas, the estimate for total abundance of 0-age sole during the May-June period on the open coast was about 643 $\times$ 10^5, considerably higher than the estimate for the five estuaries, 140 $\times$ 10^5. Most of the fish caught during this period, however, were transforming or recently metamorphosed juveniles that could have entered estuaries later in the year. This may in part explain the 17-fold decrease in average abundance of small sole along the open coast between 16-23 May ($\bar{x}$ = 0.039, n = 18, s = 0.11) and 28-29 June ($\bar{x}$ = 0.002, n = 29, s = 0.004) in the vicinity of Tillamook and Siletz Bays. Our estimate of total abundance along the coast in June is 70 $\times$ 10^5, about half the estimate for the five estuaries about a month and one-half earlier. Because of our small sample sizes, lack of sampling in some estuaries and open coast areas, and temporal differences (and associated mortality) among samples, these estimates must be considered crude. Nevertheless, they suggest that shallow waters of the open coast are important initial settling areas for English sole and that both estuaries and the open coast are nursery grounds for fully transformed 0-age sole.

We need data on the growth and survival from estuarine and open coastal areas to evaluate their importance as nursery grounds and to assess their relative contributions to the commercially harvested and spawning population. Olsen and Pratt (1973) used parasites as indicators of English sole nursery grounds. The incidence of *Echinorhynchus lageniformis*, an acanthocephalan that they considered was acquired only in estuaries, averaged 29.9% in 0-age English sole <117 mm SL captured in Yaquina Bay and 28.5% in 0-age fish collected offshore at depths of 10-80 m near the entrance of Yaquina Bay during November and December, a period after most 0-age fish had emigrated from the bay. They con-

cluded from these similar incidences of infection that there was no sizable influx of 0-age English sole to their offshore study area other than from estuarine nursery grounds. Their results imply that any 0-age fish that reside along the open coast during the spring and summer have much higher mortality rates than estuarine residents and do not contribute significantly to the offshore population of 0-age fish.

Growth rates of 0-age English sole from Moolack Beach and Yaquina Bay, however, do not support this hypothesis. They appear to be similar (Rosenberg 1982; Table 4). Our catch curves (Fig. 5C, D) also provide no evidence for grossly higher mortality rates at Moolack Beach. The total declines in abundances per m^2 are fairly similar for English sole 50-100 mm, presumably a size range that occurs after immigration into the estuary but before emigration of larger sizes out of the estuary in the fall.

The fact that 0-age English sole immigrate from offshore into estuaries where they are found in high concentrations suggests that this behavior is adaptive. Standing stocks and productivity of small benthic food organisms are undoubtedly higher in estuaries than along the open coast, but because of the higher concentrations of young flounder in Yaquina Bay than Moolack Beach (Fig. 5), competition for food probably results in similar growth rates in these two habitats. The rapid decreases in the estuarine densities of 0-age English sole during the fall and winter months are evidence of emigration out of estuaries to offshore areas. In Yaquina Bay, we found a decrease in density of 0-age fish in the late fall as well as a decrease in average size at this time. Frequently age-0 (20-55 mm) and age-I (75-115 mm) fish were both present in the winter, with the age-I fish disappearing entirely from catches in the spring. Westrheim (1955) and Olsen and Pratt (1973) also found decreases in catch per effort and average sizes of young English sole that indicated definite emigration from Yaquina Bay after October. Forsberg et al. (1975)[10] reported emigration of English sole from Tillamook Bay in early fall with few individuals remaining in November.

According to Bayer (1981), small English sole were common at intertidal stations in Yaquina Bay most of the year, but they were absent during November and were less common during other fall months. Toole (1980) also found that English sole disappeared from intertidal areas in early fall at an average size of 68 mm SL and subsequently resided in subtidal channels until they were about 120 mm SL in Humboldt Bay. He associated these different distributions with changes in feeding habits, and possibly with a reduction in intraspecific competition among small and large 0-age English sole. Indeed, emigration out of bays and estuaries in the fall may be related to limitations in the carrying capacity for high densities and standing stocks of young English sole.

We conclude that estuarine and offshore nursery grounds combine to significantly increase the survival and total population size of 0-age fish. Utilization of these two diverse habitats may also improve the chances for good survival of young fish from at least one habitat even when adverse conditions affect the other.

[10]Forsberg, B. O., J. A. Johnson, and S. M. Klug. 1975. Identification and notes on food habits of fish and shellfish in Tillamook Bay, Oreg. Fish Comm. Oreg. Contract Rep., 85 p.

LITERATURE CITED

AHLSTROM, E. H., AND H. G. MOSER.
1975. Distributional atlas of fish larvae in the California Current region: flatfishes, 1955 through 1960. Calif. Coop. Oceanic Fish. Invest., Atlas 23:1-207.

ALDERICE, D. F., AND C. R. FORRESTER.
1968. Some effects of salinity and temperature on early development and survival of the English sole (*Parophrys vetulus*). J. Fish. Res. Board Can. 25:495-521.

BAYER, R. D.
1981. Shallow-water intertidal ichthyofauna of the Yaquina estuary, Oregon. Northwest Sci. 55:182-193.

BUDD, P. L.
1940. Development of the eggs and early larvae of six California fishes. Calif. Dep. Fish Game, Fish Bull. 56, 53 p.

CAREY, A. G., JR., AND H. HEYOMOTO.
1972. Techniques and equipment for sampling benthic organisms. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters, bioenvironmental studies, p. 378-408. Univ. Wash. Press, Seattle.

CHOI, B.
1975. Pollution and tidal flushing predictions for Oregon's estuaries. M.S. Thesis, Oregon State Univ., Corvallis, 163 p.

CREUTZBERG, F., A. TH. G. W. ELTINK, AND G. J. VAN NOORT.
1978. The migration of plaice larvae, *Pleuronectes platessa*, into the western Wadden Sea. *In* D. S. McLusky and A. J. Berry (editors), Physiology and behavior of marine organisms, p. 243-252. Proc. 12th Eur. Symp. Mar. Biol., Stirling, Scotl. Pergamon Press, N.Y.

DEMORY, R. L.
1971. Depth distribution of some small flatfishes off the northern Oregon-southern Washington coast. Res. Rep. Fish. Comm. Oreg. 3:44-48.

DE VEEN, J. F.
1978. On selective tidal transport in the migration of North Sea plaice (*Pleuronectes platessa*) and other flatfish species. Neth. J. Sea Res. 12:112-147.

ELDRIDGE, M.
1970. Larval fish survey of Humboldt Bay. M.S. Thesis, Humboldt State Coll., Arcata, 52 p.

FORRESTER, C. R.
1969. Results of English sole tagging in British Columbia waters. Pac. Mar. Fish. Comm. Bull. 7:1-10.

HARRY, G. Y., JR.
1959. Time of spawning, length at maturity, and fecundity of

the English, petrale, and Dover soles (*Parophrys vetulus*, *Eopsetta jordani*, and *Microstomus pacificus*, respectively). Oreg. Fish Comm., Res. Briefs 7(1):5-13.

HART, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. 80, 740 p.

HEWITT, G. R.
1980. Seasonal changes in English sole distributions: An analysis of the inshore trawl fishery off Oregon. M.S. Thesis, Oregon State Univ., Corvallis, 59 p.

JOW, T.
1969. Results of English sole tagging off California. Pac. Mar. Fish. Comm. Bull. 7:15-33.

KENDALL, A. W., JR.
1966. Sampling juvenile fishes on some sandy beaches of Puget Sound, Washington. M.S. Thesis, Univ. Washington, Seattle, 77 p.

KETCHEN, K. S.
1947. Studies on lemon sole development and egg production. Fish. Res. Board Can., Prog. Rep. Pac. 73:68-70.
1956. Factors influencing the survival of the lemon sole (*Parophrys vetulus*) in Hecate Strait, British Columbia. J. Fish. Res. Board Can. 13:647-694.

KRUSE, G. H., AND A. V. TYLER.
1983. Simulation of temperature and upwelling effects on the English sole (*Parophrys vetulus*) spawning season. Can. J. Fish. Aquat. Sci. 40:230-237.

KRYGIER, J. E., AND H. F. HORTON.
1975. Distribution, reproduction, and growth of *Crangon nigricauda* and *Crangon franciscorum* in Yaquina Bay, Oregon. Northwest Sci. 49:216-240.

KUIPERS, B.
1975. On the efficiency of a two-meter beam trawl for juvenile plaice (*Pleuronectes platessa*). Neth. J. Sea Res. 9:69-85.

LAROCHE, J. L., AND S. L. RICHARDSON.
1979. Winter-spring abundance of larval English sole, *Parophrys vetulus*, between the Columbia River and Cape Blanco, Oregon during 1972-75 with notes on occurrences of three other pleuronectids. Estuarine Coastal Mar. Sci. 8:455-476.

LAROCHE, J. L., S. L. RICHARDSON, AND A. A. ROSENBERG.
1982. Age and growth of a pleuronectid, *Parophrys vetulus*, during the pelagic larval period in Oregon coastal waters. Fish. Bull., U.S. 80:93-104.

LAROCHE, W. A., AND R. L. HOLTON.
1979. Occurrence of 0-age English sole, *Parophrys vetulus*, along the Oregon coast: An open coast nursery area? Northwest Sci. 53:94-96.

MISITANO, D. A.
1970. Aspects of the early life history of English sole (*Parophrys vetulus*) in Humboldt Bay, California. M.S. Thesis, Humboldt State Coll., Arcata, 57 p.
1976. Size and stage of development of larval English sole, *Parophrys vetulus*, at time of entry into Humboldt Bay. Calif. Fish Game 62:93-98.
1977. Species composition and relative abundance of larval and post-larval fishes in the Columbia River estuary, 1973. Fish. Bull., U.S. 75:218-222.

MUNDY, B. C.
1984. Yearly variation in the abundance and distribution of fish larvae in the coastal upwelling zone off Yaquina Head, Oregon from June 1969 to August 1972. M.S. Thesis, Oregon State Univ., Corvallis, 158 p.

MYERS, K. W. W.
1980. An investigation of the utilization of four study areas in Yaquina Bay, Oregon, by hatchery and wild juvenile salmonids. M.S. Thesis, Oregon State Univ., Corvallis, 234 p.

OLSEN, R. E., AND I. PRATT.
1973. Parasites as indicators of English sole (*Parophrys vetulus*) nursery grounds. Trans. Am. Fish. Soc. 102:405-411.

PATTIE, B. H.
1969. Dispersal of English sole, *Parophrys vetulus*, tagged off the Washington coast in 1956. Pac. Mar. Fish. Comm. Bull. 7:11-14.

PEARCY, W. G., AND S. S. MYERS.
1974. Larval fishes of Yaquina Bay, Oregon: A nursery ground for marine fishes? Fish. Bull., U.S. 72:201-213.

PORTER, P.
1964. Notes on fecundity, spawning and early life history of petrale sole (*Eopsetta jordani*) with descriptions of flatfish larvae collected in the Pacific Ocean off Humboldt Bay, California. M.S. Thesis, Humboldt State Coll., Arcata, 98 p.

RICHARDSON, S. L., AND W. G. PEARCY.
1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull., U.S. 75:125-145.

ROSENBERG, A. A.
1982. Growth of juvenile English sole, *Parophrys vetulus*, in estuarine and open coastal nursery grounds. Fish. Bull., U.S. 80:245-252.

ROSENBERG, A. A., AND J. L. LAROCHE.
1982. Growth during metamorphosis of English sole, *Parophrys vetulus*. Fish. Bull., U.S. 80:150-153.

SIMS, C. W., AND R. H. JOHNSON.
1974. Variable-mesh beach seine for sampling juvenile salmon in Columbia River estuary. Mar. Fish. Rev. 36(2):23-26.

SMITH, J. G., AND R. J. NITSOS.
1969. Age and growth studies of English sole, *Parophrys vetulus*, in Monterey Bay, California. Pac. Mar. Fish. Comm. Bull. 7:73-79.

TATE, M. W., AND R. C. CLELLAND.
1957. Nonparametric and shortcut statistics in the social, biological, and medical sciences. Interstate Printers and Publishers Inc., Danville, IL, 171 p.

TOOLE, C. L.
1980. Intertidal recruitment and feeding in relation to optimal utilization of nursery areas by juvenile English sole (*Parophrys vetulus*: Pleuronectidae). Environ. Biol. Fishes 5: 383-390.

TSURUTA, Y.
1978. Field observations on the immigration of larval stone flounder into the nursery ground. Tohoku J. Agric. Res. 29: 136-145.

VAN CLEVE, R., AND S. Z. EL-SAYED.
1969. Age, growth, and productivity of an English sole (*Parophrys vetulus*) population in Puget Sound, Washington. Pac. Mar. Fish. Comm. Bull. 7:51-71.

WESTRHEIM, S. J.
1955. Size composition, growth and seasonal abundance of juvenile English sole (*Parophrys vetulus*) in Yaquina Bay. Oreg. Fish. Comm. Res. Briefs 6(2):4-9.

ORGANIC AND TRACE METAL LEVELS IN OCEAN QUAHOG, *ARCTICA ISLANDICA LINNÉ*, FROM THE NORTHWESTERN ATLANTIC

FRANK W. STEIMLE,[1] PAUL D. BOEHM,[2] VINCENT S. ZDANOWICZ,[1] AND RALPH A. BRUNO[1]

ABSTRACT

Chemical contamination of biological resources is an important problem for resource managers. This study reports on body burden levels of several contaminants of concern: polychlorinated biphenyls (PCB), polynuclear aromatic hydrocarbons (PAH) of both petroleum and combustion sources, total petroleum hydrocarbons, and seven trace metals (Ag, Cd, Cr, Cu, Ni, Pb, and Zn) in a resource species, the ocean quahog, collected between Virginia and Nova Scotia. Organic and trace metal contaminants were detected, at low levels, in all samples examined, with highest levels being generally found in samples from the inner New York Bight and Rhode Island Sound. The highest PCB and PAH values were 27 and 55 ppb, respectively; Ag, Cd, and Cr values were generally <5 μg/g dry weight; Cu, Ni, and Pb generally <15 μg/g dry weight with a few exceptions; and Zn ranged from 50 to 153 μg/g dry weight.

The ocean quahog, *Arctica islandica* Linné, is a large, bivalve mollusc found on both sides of the North Atlantic. In the northwestern Atlantic, it occurs from just north of Cape Hatteras, NC, to Newfoundland, Nova Scotia, being most abundant on the middle to outer continental shelf at depths between about 30 and 150 m (Merrill et al. 1969). The species is edible and some commercial harvesting has occurred since 1943 in the Rhode Island area; however, intensive fishing for this species did not begin until the 1970s when surf clam, *Spisula solidissima* (Dillwyn), stocks, an inshore species, were drastically reduced by overfishing (Ropes 1979).

Arctica islandica generally inhabit silty sand sediments of the middle to outer continental shelf that are less influenced by waves and strong currents than shallower areas. Areas of silty sand are thought to be at least partially depositional in nature, i.e., fine organic-rich particles tend to accumulate. It is generally agreed that many chemical pollutants, introduced to the marine environment via impacted estuaries and coastal areas, ocean dumping, and atmospheric sources, often are bound to and associated with fine organic and inorganic particle aggregates, both in the water column and at the sediment surface. These aggregates ultimately can accumulate in these natural depositional areas as the results of some recent studies show that contaminants apparently are accumulating in silty areas relatively remote from most possible sources, e.g., organic contaminants found south of Cape Cod, MA, in the middle to outer continental shelf (Boehm 1983a). Some authors have also reported a trend of increasing sediment trace metal levels with depth on the Middle Atlantic shelf (Harris et al. 1977), but the specific sources of these contaminants are still unknown.

Because *A. islandica* is a common, sedentary, long-lived (Thompson et al. 1980) inhabitant of these silty sands that frequently contain higher levels of contaminants than coarser sands, the species may be particularly susceptible to contamination. Wenzloff et al. (1979) reported "greater average concentration of silver, arsenic, cadmium, copper, and zinc . . . in ocean quahogs than in surf clams" for the Middle Atlantic. Surf clams are generally found in shallower, medium sand areas. Thus, *A. islandica* may be a good offshore "indicator" species to monitor for trends in marine chemical pollution. Although some studies on contaminant body burdens of *A. islandica* have been reported (ERCO 1978[3]; Sick 1978, 1981; Wenzloff et al. 1979; Reynolds 1979; Payne et al. 1982), these studies have been limited generally to a particular restricted area, have not examined both types of contaminants or only a few components of each contaminant class, or have examined only certain tissues, not whole body levels.

The present study provides body burden data over

[1]Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732.
[2]Battelle, New England Marine Research Laboratory, 397 Washington Street, Duxbury, MA 02332.

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[3]ERCO (Energy Resources Company). 1978. New England OCS Environmental Benchmark. Draft Final Rep., Vol. II, to U.S. Dep. Inter., Bur. Land Manage., Miner. Manage. Serv., 628 p.

a wide range of this species' occurrence in the northwestern Atlantic and includes information on organic, i.e., polychlorinated biphenyls (PCB), polynuclear aromatic hydrocarbons (PAH) from combustion and petroleum sources, and bulk levels of the petroleum hydrocarbon (PHC) class, and seven trace metal contaminants. The study includes the first known set of PCB data for this species.

MATERIALS AND METHODS

Ocean quahog samples were obtained at random stations from wide areas on the continental shelf of the northwestern Atlantic (Fig. 1). These were collected from annual, summer hydraulic dredge shellfish surveys of NOAA's Northeast Fisheries Center from 1981 and 1982. At most stations, 10-12 medium-sized clams were selected, as available. Half of the collection was prepared for organic analysis by wrapping them in aluminum foil that had been prewashed with spectral grade acetone followed by dichloromethane; the remaining half for trace metals were placed in polyethylene plastic bags. All were quickly frozen at −20°C. In certain areas where there were not sufficient samples at a particular station to provide material for both organics and trace metal analyses, samples were collected at a nearby station, with similar environmental characteristics, to complete the collection for the area. These paired station samples were not intermixed.

Chemical Analysis - Organics

In the laboratory, the thawed whole meats of each of the five or six individual clams in each station sample were removed from the shells, pooled, and homogenized in a high-speed blender. A 100 g (wet weight) aliquot was removed from the homogenate and processed according to the extraction, fractionation, and analytical methodology described by Warner (1976), as modified by Boehm et al. (1982). After aqueous caustic (0.5N KOH) digestion of the tissue for 12 h, the digestate was back-extracted three times with hexane. The hexane extract was concentrated by rotary evaporation, then fractionated on a 5% deactivated alumina/activated silica gel column. The first eluting fraction from the alumina/silica column (f_1) contained the saturated PHC; the second fraction (f_2) contained the PCB and PAH. Quantitation procedures closely followed those by Boehm (1983b). PHC factors were quantified using the internal standard method whereby all peaks are quantified relative to androstane in the f_1 fraction and 0-terphenyl in the f_2 fraction.

PCBs were quantified relative to the internal standard tetrazene (2, 3, 5, 6 tetrachloronitrobenzene). The average relative response factors of two or three isomers in each of the di-, tri-, tetra-, penta-, hexa-, hepta- and octachlorobiphenyls groups were applied to the sum of the peaks in each grouping. Thus, PCBs were quantified by isomer group rather than according to the Aroclor[4]-type quantification (Duinker et al. 1980, 1983; Boehm 1983b). PHCs were determined by the total of f_1 and f_2 fractions, as analyzed by high resolution (fused silica capillary) gas chromatography with flame ionization detection (GC^2/FID). A Hewlett Packard model 5840A gas chromatograph was used for all GC^2 determinations. A 30 m fused silica SE-30 (0.25 mm i.d.; J and W Scientific) column was used to analyze the saturated hydrocarbon (f_1) fraction. A 30 m SE-52 fused silica column was used to analyze the aromatic/olefinic (f_2) fraction by GC^2/FID and the same fraction by gas chromatograph/mass spectrometer (GC/MS) (see below). The f_2 fractions were analyzed by GC^2/ECD (electron capture detection) to obtain the PCB concentrations. PCBs were analyzed on a 30 m SE-52 fused silica column. The f_2 fraction was also analyzed by a Finnegan MAT model 4530 computer-assisted GC/MS system for PAH determinations. GC/MS conditions were as follows: ionization voltage, 70 ev; electron multiplier voltage 2,000 volts; scan conditions 45-450 amu at 400 amu/s.

Chemical Analysis - Trace Metals

Whole clams, 5 or 6 per station, were thawed, and the whole body removed from the shells. Each individual clam was weighed in Pyrex beakers and dried for 16-20 h at 105°C. Twenty mL of 70% trace metal grade nitric acid were added to each beaker, which was covered with a Pyrex watch glass and heated (70° -75°C) on a ceramic hot plate until dry. After cooling to room temperature, another 20 mL of concentrated nitric acid were added and the dissolution continued. After 3 or 4 repeated acid additions and evaporations, 10 mL of 30% hydrogen peroxide were added, the solutions evaporated to near dryness and removed from the heat. When cooled, samples were filtered through Whatman #4 filter paper and brought to a final volume of 25 mL in a Pyrex glass-stoppered graduated cylinder by adding 5% (w/v) nitric acid. Analysis was performed on a Perkin Elmer model 5000 atomic absorption (AA) spectrophotometer employing an air-acetylene flame and conven-

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

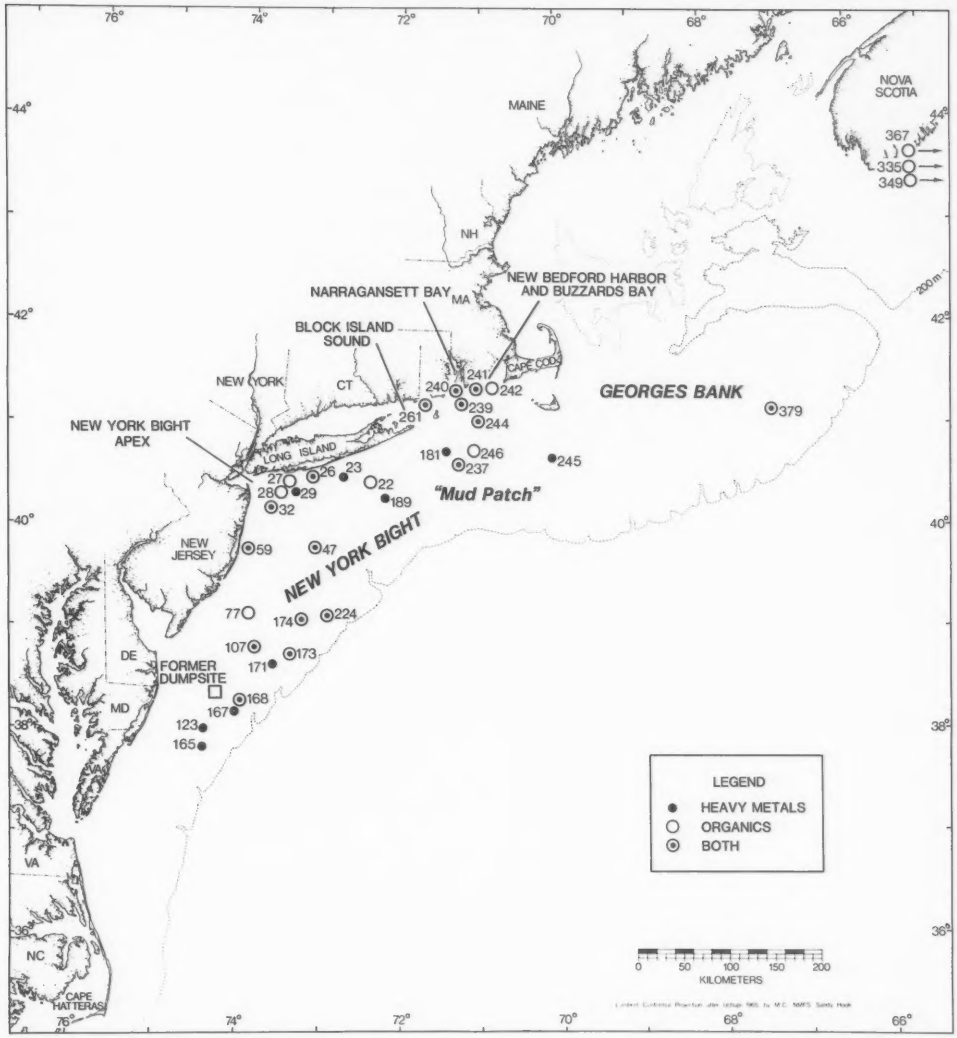

FIGURE 1.—Station locations' collections of *Arctica islandica*. Stations 367, 335 and 349 are on the Scotian Shelf at the following coordinates: Station 367 (lat. 43°44′N, long. 61°08′W), Station 335 (43°25′N, 61°42′W) and Station 349 (43°21′N, 61°23′W).

tional AA techniques. Reagent blanks were carried through the same procedure. All reagents used were of trace metal analytical grade. Deionized water was of 18 megohm purity. The National Bureau of Standards (NBS) SRM 1566, freeze-dried oyster homogenate, was used as the tissue standard. Recoveries were at least 80% of this standard in all cases.

RESULTS

The analytical results for organic contaminants are presented in Tables 1 (PHC and PCB) and 2 (PAH). PHC values are given as total saturated and aromatic hydrocarbons as determined by GC[2]. PCB values are given as total tri-, tetra-, penta-, hexa-, and hepta-

TABLE 1.—PHC (petroleum hydrocarbon) and PCB (polychlorinated biphenyl) levels in northwestern Atlantic *Arctica islandica*.

Area and station	PHC (μg/g wet weight)			PCB (ng/g wet weight)					
	Saturated	Aromatic	Total	Cl_3	Cl_4	Cl_5	Cl_6	Cl_7	Total
Inshore New York Bight									
22	0.2	1.3	1.5	4.8	5.1	1.6	4.4	0.2	16.1
26	6.0	0.9	6.9	0.4	0.3	0.2	0.5	0.1	1.5
27	0.4	0.8	1.2	7.2	2.8	1.6	1.8	<0.1	13.4
28	0.2	0.9	1.1	6.7	4.2	2.6	6.5	0.1	20.2
32	3.2	4.1	7.3	5.4	5.1	4.1	10.7	0.7	26.8
47	<0.1	0.2	0.2	1.1	0.4	0.1	0.3	—	1.9
59	3.1	1.5	4.6	3.4	3.6	3.0	5.7	0.5	16.4
Offshore NJ-VA									
77	1.7	0.7	2.4	5.6	1.2	2.9	2.3	0.3	12.2
107	0.2	0.8	1.0	8.0	1.7	0.8	2.8	0.2	13.3
168	0.2	1.1	1.3	2.3	1.3	1.0	3.5	0.5	8.5
173	0.4	0.5	0.9	4.4	4.5	1.3	3.4	—	14.0
174	1.0	0.3	1.3	2.6	0.8	0.4	1.5	<0.1	5.5
224	1.7	0.2	1.9	2.3	1.5	0.5	0.5	<0.1	4.9
Inshore S. New England									
237	0.1	0.8	0.9	1.0	0.6	<0.1	<0.1	—	1.7
246	1.2	0.4	1.6	2.0	2.8	2.2	1.5	—	8.5
244	2.2	1.3	3.5	4.9	9.5	2.3	3.8	—	20.4
261	2.0	0.4	2.4	3.4	3.5	2.1	3.1	<0.1	12.1
239	2.9	1.1	4.0	1.4	2.1	1.6	1.9	<0.1	7.0
240	2.8	0.9	3.7	2.2	2.6	2.7	3.5	<0.1	11.0
241	2.3	1.6	3.9	4.1	6.6	6.2	6.3	0.2	23.2
242	1.9	1.8	3.7	2.9	4.6	5.9	6.5	0.2	20.1
Georges Bank									
379	0.8	1.1	1.9	0.7	1.2	0.9	1.0	<0.1	3.8
Scotian Shelf									
367	0.6	0.2	0.8	0.8	0.5	0.4	0.3	0.3	2.2
335	1.1	0.1	1.2	0.9	0.4	0.5	2.3	0.1	4.2
349	4.5	0.6	5.1	0.8	0.9	0.4	0.1	—	2.2

chlorobiphenyls (Cl_3-Cl_7), as well as total PCB. PAH values are presented as individual compounds (e.g., napthalene) or as homologous series (ΣN). Table 3 lists the mean trace metal concentrations and standard deviations; data are presented on a dry weight basis to simplify comparisons with other studies.

DISCUSSION

PCB levels observed in this survey ranged from 2 to 30 ng/g (ppb) wet weight (Table 1). These values are in general agreement with other data reported for PCB levels in other coastal bivalves (Giam et al. 1976; Goldberg 1978; Gadbois 1982), but are lower than those (to 400 ppb) reported for estuarine species (Goldberg 1978; MacLeod et al. 1981; O'Connor et al. 1982; ERCO 1983). However, we have found little data on PCB levels in offshore molluscs nor any other data on PCB levels in *A. islandica* for comparison. None of the *A. islandica* levels approach the current 2 ppm (= 2,000 ppb) U.S. Food and Drug Administration (FDA) "seafood action limit" for human consumption.

In spite of the wide geographical range sampled, PCB levels were relatively uniform with only an order of magnitude difference between the high and low values. Clearly the Georges Bank (station 379) and remote Nova Scotia (stations 367, 335, 349) ocean quahogs were minimally contaminated, with their levels (2-5 ppb) reflecting the global PCB transport phenomena. The ocean quahogs in the nearshore New York Bight, Rhode Island Sound, and Buzzards Bay were more contaminated, with values up to 25 ppb. It is not surprising as previous biogeochemical studies in the western North Atlantic have clearly shown that several major urban pollutant sources influence the nearshore environment. For example, inputs of PCBs are specifically known to occur in the New York Bight, from esturine fluxes and via direct ocean dumping (Boehm 1983b) and in Buzzards Bay, MA, from industrial inputs to the New Bedford Harbor region (Weaver 1982). Somewhat surprising were the elevated levels at some stations on the outer New Jersey shelf (12-16 ppb) and in the Hudson Canyon area (20 ppb). Offshore transport of PCB material towards these stations via riverine fluxes followed by southerly transport along the New Jersey shore and down-canyon transport of ocean-dumped material are possible modes of transport to these stations (Boehm 1983b).

TABLE 2.—PAH (polynuclear aromatic hydrocarbon) levels in northwestern Atlantic *Arctica islandica* (ng/g wet weight).

Area and station	N	ΣN	P	ΣP	ΣDBT	ΣF	Σ202	Σ228	Σ252	B(a)P	ΣPAH	PPI[1]
Inshore New York Bight												
22	nd	nd	4.0	11.9	2.0	1.2	5.5	1.1	<1	<1	23	40
26	nd	nd	1.1	1.1	nd	nd	1.1	nd	nd	nd	3.3	0
27	1.0	4.5	2.1	9.1	2.7	1.2	2.7	<1	<1	nd	22	54
28	9.1	12.0	1.3	5.2	<1	nd	1.8	nd	nd	nd	20	72
32	nd	nd	3.9	12.4	nd	nd	11.1	14.1	17.3	6.0	55	7
47	4.3	5.1	2.9	2.9	nd	nd	3.1	3.0	4.0	2.0	18	28
59	1.0	5.3	1.0	11.5	<1	nd	1.5	<1	nd	nd	20	77
Offshore NJ-VA												
77	<1	3.7	3.3	9.2	<1	1.0	2.4	<1	nd	nd	18	65
107	<1	6.7	2.5	10.0	2.5	3.5	1.5	<1	<1	nd	26	77
168	nd	nd	1.8	1.8	nd	nd	2.4	nd	nd	nd	4.2	0
173	1.3	5.9	1.8	6.2	1.3	2.0	2.3	<1	nd	nd	19	72
174	<1	4.0	1.0	5.0	<1	nd	4.0	1.0	1.0	nd	16	56
224	1.4	6.1	2.0	7.8	2.1	1.5	1.3	<1	<1	<1	21	74
Mud Patch												
237	<1	<1	2.8	5.0	<1	nd	5.7	3.7	5.4	2.5	19	31
246	nd	11.9	2.2	11.5	1.0	1.3	3.3	nd	nd	nd	29	81
Inshore S. New England												
244	nd	nd	nd	nd	2.4	nd	1.7	<1	<1	<1	6.1	39
261	nd	nd	3.6	9.2	<1	<1	3.3	nd	nd	nd	15	51
239	nd	nd	1.6	1.9	nd	nd	2.9	<1	1.2	<1	7.0	4
240	<1	3.3	1.8	5.6	<1	<1	2.8	<1	<1	<1	16	51
241	nd	nd	nd	5.0	nd	nd	4.0	1.0	1.0	<1	12	42
242	nd	nd	<1	<1	nd	nd	1.5	nd	nd	nd	2.5	40
Georges Bank												
379	nd	nd	<1	<1	nd	nd	<1	nd	nd	nd	<1	0
Scotian Shelf												
367	1.0	1.0	1.5	1.5	nd	nd	1.1	nd	nd	nd	3.6	28
335	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	0
349	4.3	5.1	2.9	2.9	nd	nd	3.1	3.0	4.0	2.0	18	28

Wet weight concentrations = dry weight concentration ÷ 7.
N = naphthalene.
ΣN = total naphthalenes (C_0-C_4).
P = phenanthrene.
ΣP = total phenanthrenes (C_0-C_4).
ΣDBT = total dibenzothiophenes (C_0-C_3).
ΣF = total fluorenes (C_0-C_3).
Σ202 = fluoranthene + pyrene.
Σ228 = benzanthracene + chrysene.
Σ252 = benzofluoranthenes + benzopyrenes.
B(a)P = benzo(a)pyrene.
nd = not detected (<1 ng/g wet weight).

$$\text{PPI} = \text{percent petroleum index} = \frac{\Sigma N + \Sigma DBT + (\Sigma P - P) + \Sigma F}{\Sigma PAH}$$

$$\Sigma PAH = \Sigma N + \Sigma P + \Sigma DBT + \Sigma F + \Sigma 202 + \Sigma 252 + \Sigma 228$$

[1]From Boehm (1983a).

Trends in the PHC and PAH data reveal large-scale homogeneity in the concentrations observed. PAH levels ranged from nondetectable to 55 ppb, the highest values occurring at the station 32 samples from the New York Bight, where the highest PCB level (27 ppb) was also observed. Although our sampling on Georges Bank consisted of only one station, results were similar to those of a more extensive study by Payne et al. (1982), the only other study of *A. islandica* we could locate that includes PHC data. If the entire Northeast region is considered a sample set, then the PAH values were 16.7 ± 12.0. However, the composition of the PAH which comprises the total PAH number varied considerably, ranging from 0 to 81% "petroleum" PAH (Table 2). The percent petroleum index (PPI), developed by Boehm (1983a, b), estimates the relative contributions of uncombusted fossil fuels, e.g., petroleum, and from combustion sources to the total PAH assemblage. This indice, presented in Table 2, is based on the relative abundance of petroleum constituents, such as naphthalene, flourenes, dibenzothiophenes, and alkylated phenanthrenes, to the total PAH mix. The differences in PPI values for the various samples cannot, at this time, be ascribed to specific transport or selective uptake factors. However, a knowl-

TABLE 3.—*Arctica islandica* trace metal body burdens (mean and standard deviation, μg/g-dry weight) in areas of the northwest Atlantic; N = number of individual clams examined at each site. Results of analysis of SRM 1566 are also included; 5-8 NBS (National Bureau of Standards) samples were examined for each metal (nd = nondetectable).

Area and station	N	Ag		Cd		Cr		Cu		Ni		Pb		Zn	
		X	±SD	X	±SD	X	±SD	X	±SD	X	±SD	X	±SD	X	±SD
Georges Bank															
379	6	0.79	0.25	1.36	0.33	3.07	1.38	10.30	2.22	3.46	1.17	4.08	2.07	61.8	11.4
Nantucket															
245	5	0.96	0.09	2.75	0.66	2.98	0.83	7.25	1.41	9.54	3.81	5.02	2.21	88.3	21.3
S. New England															
237	6	2.65	2.08	3.22	0.65	2.72	0.65	12.76	3.30	27.19	8.18	6.90	1.87	153.9	87.6
181	6	1.14	0.95	3.49	1.39	2.24	0.23	11.70	2.97	21.84	7.22	11.03	4.48	124.7	30.8
244	6	0.56	0.14	1.36	0.47	2.19	1.02	6.49	3.29	4.47	1.75	2.99	1.33	84.1	25.7
Rhode Island Sound															
239	6	0.79	0.25	1.36	0.33	3.07	1.38	10.30	2.22	3.46	1.17	4.08	2.07	61.8	11.4
240	6	1.76	0.65	1.39	0.48	4.02	1.26	11.47	2.92	6.28	1.61	6.71	2.51	87.4	12.8
241	6	1.59	0.93	0.96	0.14	3.96	2.23	12.47	3.80	5.83	2.42	4.61	1.71	126.3	55.4
Block Island Sound															
261	6	1.53	1.82	1.94	0.68	4.56	0.33	10.22	1.55	11.64	3.28	10.17	2.48	101.9	32.6
S. Long Island															
189	6	0.74	0.60	2.48	0.63	1.88	0.59	8.78	0.94	18.73	4.75	3.30	0.80	128.4	35.2
23	6	1.18	0.53	2.17	0.67	1.09	0.19	10.31	3.27	17.28	6.07	3.41	1.12	120.2	19.6
26	6	0.84	0.45	1.43	0.56	5.47	1.22	15.78	5.83	9.87	2.73	8.66	3.25	117.6	35.7
29	6	5.25	1.64	1.06	0.29	4.78	3.35	13.65	3.20	8.93	5.06	9.67	4.11	100.7	49.9
New Jersey Shelf															
32	6	0.52	0.26	0.67	0.35	2.38	0.20	8.16	5.38	4.47	2.90	3.46	2.24	50.2	22.0
47	5	0.53	0.36	1.20	0.42	1.46	0.83	8.37	2.49	9.87	5.09	3.11	0.87	84.1	31.8
59	3	0.44	0.15	0.23	0.05	0.90	0.09	6.01	1.37	6.01	1.68	1.64	0.28	62.2	18.8
174	6	1.50	0.91	2.19	0.93	1.87	0.65	4.08	0.82	7.79	2.70	4.16	1.60	50.8	6.0
224	6	0.46	0.13	3.06	0.91	1.78	0.43	5.63	1.02	14.91	6.92	5.60	2.23	91.9	33.9
Delmarva Shelf															
107	6	0.39	0.25	1.87	0.62	2.44	0.90	4.16	1.02	10.27	2.52	4.80	2.77	58.9	14.2
173	5	0.44	0.30	2.34	1.54	1.62	0.48	4.46	1.76	11.14	4.94	4.35	2.32	61.4	26.2
171	6	0.51	0.12	1.66	0.56	1.71	0.44	5.25	1.57	10.91	3.21	3.55	1.09	75.8	31.8
167	6	0.52	0.29	1.59	0.48	1.98	0.56	7.04	4.36	9.45	4.20	3.54	1.21	76.2	43.4
168	5	2.22	1.36	3.08	1.03	2.38	0.68	5.19	1.79	13.74	5.34	6.51	2.57	74.6	14.8
123	6	2.40	1.68	2.53	0.58	3.34	1.01	4.98	1.16	14.13	3.95	5.91	1.58	77.9	20.6
165	5	0.54	0.36	2.09	0.68	2.36	0.78	6.44	2.39	11.48	4.78	4.35	2.21	74.4	28.5
NBS SRM 1566															
—	8	0.71	0.24	2.86	0.19	1.07	0.52	49.50	4.00	1.72	0.35	nd	—	772.0	53.0

edge of a baseline PPI value can be important for discerning the source of any change in contaminant levels in benthic animals.

In a similar manner, the PCB value has been separated, by virtue of the use of capillary GC, into isometric groupings (Table 1). Again, there were differences in PCB composition between samples. For example, samples from stations 22, 28, 32, and 244 were largely comprised of tri-, tetra-, and hexachloro PCB isomers, while those from stations 107 and 27 contained significantly greater quantities of the trichlorobiphenyls. Aroclor 1016 and 1242 contain proportionately more of the Cl_1 to Cl_4 isomers while Aroclor 1254 contains a greater abundance of Cl_4 to Cl_6 isomers. In the future, it may be possible to ascribe the differences in the PCB composition in animals to possible sources through capillary GC/ECD measurements.

Highest trace metal concentrations in *A. islandica* varied from metal to metal (Table 3); however, highest mean Ag, Cr, Cu, and Pb concentrations were found in New York Bight (stations 26 and 29), while Ni and Zn were highest in the "Mud Patch" (stations 181 and 237) with the highest Cd values off Delaware (Table 3). Lowest concentrations, overall, were observed at midshelf stations off New Jersey and Maryland (with the exception of stations 167, 168, and 123 that could have been influenced by dumping at a nearby dumpsite) and station 379, on Georges Bank. Comparison of these data with those of Wenzloff et al. (1979), who analyzed metals in ocean quahogs from the New York Bight to an area off Chesapeake Bay, was attempted for temporal trends. Unfortunately, the Wenzloff et al. (1979) data were obtained from only foot muscle composites of 5 or 6 quahogs at each station, reported as means of all composites per half degree of latitude; hence, a direct comparison was not possible. The geographic pattern, a decrease in metal concentrations with latitude believed present in the Middle Atlantic Bight

by Wenzloff et al. (1979), was not apparent from the present data or from the studies summarized in Table 4. Results of other studies involving whole body analysis (Table 4) suggest that Cd, Ni, and Zn could also be high on Georges Bank; otherwise, the values presented do not support any consistent latitudinal trends.

Results indicate, however, on a local level, elevated trace metal levels were also usually associated with known areas of inputs, e.g., waste dumpsites or adjacent to heavily industrialized coastal areas, such as the New York Bight apex (station 29), or natural depositional areas where trace metals from unknown sources are apparently accumulating, e.g., the "Mud Patch" (stations 181, 237).

The uptake and accumulation of trace metals by marine organisms are known to be affected by a number of variables. These variables include season, age, size, temperature, and interactive effects of several metals (Phillips 1977), and can be sources of some of the variability shown between the results of studies in the same area. Methodology is another source of variability between the results of each study, especially when intercalibrated results with standards are not available. It is interesting to note that an expected close correlation between trace metal levels in the sediment and in *A. islandica* tissues was not evident in at least one study (Reynolds 1979), suggesting that the water and food or other suspended material could be the primary source of contaminants to this filter-feeding species.

In conclusion, a set of measurements of several organic and seven trace metal contaminant levels in the commercially valuable ocean quahog have been obtained from a wide range of northwestern Atlantic locations. This set can be used as a base to monitor long-term changes in the assimilated levels and distributions of these compounds in this species and the risk to its health of future use as food. The levels found were well below the FDA seafood action limit, but elevated values were associated with impacted coastal habitats and possibly waste dumpsites.

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TABLE 4.—Comparison of mean trace metals levels ($\mu g\ g^{-1}$ dry wt.) in *Arctica islandica* of the northwest Atlantic.

Area and reference	Ag	Cd	Cr	Cu	Ni	Pb	Zn	Tissue type
Georges Bank-Nantucket								
Sick (1978)	0.1	1.1	0.9	3.5	12.4	0.35	252	Whole body
Erco (1978)		5.1	3.9	7.6	21.0	1.00	260	Whole body
Payne et al. (1982)		4.5	1.7	5.4	27.0	3.50	150	Whole body
Present study - stn. 379	0.8	1.4	3.1	10.3	3.5	4.1	62	Whole body
Block Island Sound								
Steimle et al. (1976)		1.8		31	18.0	18.0	183	Whole body
Rogerson and Galloway (1979)[1]		1.4	8.1	23	11.8	10.2	138	Whole body
Present study - stn. 261		1.9	4.6	10	11.6	10.2	102	Whole body
Southern Long Island								
Guarimo et al. (1979)[1]		3.0	5.6	17.4	27.9	14.1	122	?
Present study - stn. 189		2.5	1.9	8.8	18.7	3.3	128	Whole body
New York Bight								
Wenzloff et al. (1979)[1]	15.8	3.5	<7.5	43.2	<5.0	9.8	107	Foot muscle
Sick (1981)	0.7	7.9		5.3				"muscle"
Present study - stn. 23, 26, 29, 32, 47	1.7	1.3	3.0	11.3	10.1	5.7	95	Whole body
Off Delaware								
Reynolds (1979)		2.4		7.7	9.0			Whole body
Present study - stn. 123, 167, 168		2.4		5.7	12.4			Whole body
Chesapeak Bight								
Wenzloff et al. (1979)[1]	9.3	3.3	<8.0	34.6	<4.7	8.5	98	Foot muscle
Present study - stn. 107 and south	1.0	2.2	2.3	5.4	11.6	4.7	71	Whole body

[1]Original wet weight data converted into dry weight by multiplying by 8.

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LITERATURE CITED

BOEHM, P. D.
1983a. Chemical contaminants in Northeastern United States marine sediments. U.S. Dep. Commer., NOAA Tech. Rep. NOS 99, 82 p.
1983b. Coupling of organic pollutants between the estuary and the continental shelf and the sediments and water column of the New York Bight region. Can. J. Fish. Aquat. Sci. 40(Suppl. 2):262-276.

BOEHM, P. D., J. E. BARAK, D. L. FIEST, AND A. A. ELSKUS.
1982. A chemical investigation of the transport and fate of petroleum hydrocarbons in littoral and benthic environments: The *Tsesis* oil spill. Mar. Environ. Res. 6:157-188.

DUINKER, J. C., M. T. J. HILLEBRAND, AND J. P. BOON.
1983. Organochlorines in benthic invertebrates and sediments from the Dutch Wadden Sea; Identification of individual PCB components. Neth. J. Sea. Res. 17:19-38.

DUINKER, J. C., M. T. J. HILLEBRAND, K. H. PALMORK, AND S. WILHELMSEN.
1980. An evaluation of existing methods for quantitation of polychlorinated biphenyls in environmental samples and suggestions for an improved method based on measurement of individual components. Bull. Environ. Contam. Toxicol. 25: 956-964.

ERCO (ENERGY RESOURCES COMPANY).
1983. Levels of selected organic pollutants in soft clams, *Mya arenaria*, from the New Bedford area. Final Rep., Contract No. NA-81-FA-C-00013, to Natl. Mar. Fish. Serv., Northeast Fish. Cent., Highlands, NJ 07732, 16 p.

GADBOIS, D.
1982. PCBs and PAH in biota. *In* R. N. Reid, J. E. O'Reilly, and V. S. Zdanowicz (editors), Contaminants in New York Bight and Long Island Sound sediments and demersal species, and contaminant effects on benthos. Summer 1980, p. 37-46. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-F/NEC-16, Woods Hole, MA.

GIAM, C. S., H. S. CHAN, AND G. S. NEFF.
1976. Concentrations and fluxes of phthlates, DDTs, and PCBs to the Gulf of Mexico. *In* H. L. Windom and R. A. Duce (editors), Marine pollutant transfer, p. 375-386. E. D. Heath and Co., Lexington, MA.

GOLDBERG, E. D.
1978. The mussel watch. Environ. Conserv. 5:101-125.

GUARINO, C. F., M. D. NELSON, AND S. S. ALMEIDA.
1979. Ocean dispersal as an ultimate disposal method. J. Water Pollut. Control Fed. 51(4):773-782.

HARRIS, R., R. JOLLY, R. HUGGETT, AND G. GRANT.
1977. Trace metals. *In* Chemical and Biological Benchmark Studies on the Middle Atlantic Outer Continental Shelf, Ch. 8. Final Rep. to Bur. Land Manage., U.S. Dep. Inter., by Va. Inst. Mar. Sci., Gloucester Point, VA 23062.

MACLEOD, W. D., L. S. RAMOS, A. J. FRIEDMAN, D. G. BURROWS, P. G. PROHASKA, D. L. FISHER, AND D. W. BROWN.
1981. Analysis of residual chlorinated hydrocarbons, aromatic hydrocarbons, and related compounds in selected sources, sinks, and biota of New York Bight. U.S. Dep. Commer., NOAA Tech. Memo. OMPA-6, Boulder, CO, 128 p.

MERRILL, A. S., J. L. CHAMBERLIN, AND J. W. ROPES.
1969. Ocean quahog fishery. *In* F. E. Firth (editor), The encyclopedia of marine resources, p. 125-129. Van Nostrand Reinhold Co., N.Y.

O'CONNOR, J. M., J. B. KLOTZ, AND T. J. KNEIP.
1982. Sources, sinks, and distribution of organic contaminants in the New York Bight ecosystem. *In* G. F. Mayer (editor), Ecological stress and the New York Bight: Science and management, p. 631-654. Estuarine Research Foundation, Columbia, SC.

PAYNE, J. R., J. L. LAMBACH, R. E. JORDAN, G. D. MCNABB, JR., R. R. SIMS, A. ABASUMAVA, J. G. SUTTON, D. GENERRO, S. GAGNER, AND R. F. SHOKES.
1982. Georges Bank monitoring program, analysis of hydrocarbons in bottom sediments and analysis of hydrocarbons and trace metals in benthic fauna. Final Rep. July 1981-May 1982 to U.S. Dep. Inter., Miner. Manage. Serv., Wash., D.C., 189 p. Science Application, Inc., La Jolla, CA 92039.

PHILLIPS, D. J. H.
1977. The use of biological indicator organisms to monitor trace metal pollution in marine and estuarine environments—a review. Environ. Pollut. 13:281-317.

REYNOLDS, B. H.
1979. Trace metal monitoring at two ocean disposal sites. U.S. Environ. Prot. Agency, ERL, Narragansett, RI, EPA 600/3-79-037, 64 p.

ROGERSON, P. F., AND W. B GALLOWAY.
1979. Preparation and characterization of a marine reference material for trace element determinations. *In* F. Jacoff (editor), Advances in marine research—Proceedings of a symposium, p. 1-8. U.S. Environ. Prot. Agency, ERL, Narragansett, RI, EPA 600/9-79-035.

ROPES, J. W.
1979. Biology and distribution of surf clams (*Spisula solidissima*) and ocean quahogs (*Arctica islandica*) off the northeast coast of the United States. *In* Proceedings of the Northeast Clam Industries: Management for the future, p. 47-66. Mass. Coop. Ext. Serv., Univ. Mass., Amherst, MA.

SICK, L. V.
1978. Trace metal analysis of zooplankton and macrobenthic tissues from Georges Bank. Sea Grant Rep. CMS-1-78, Coll. Mar. Stud., Univ. Del., Lewes, DE, 57 p.
1981. Seasonal and geographical dynamics of trace metal composition in the benthic community of the New York Bight. Final Rep. to NOAA, MESA, New York Bight Proj., Stony Brook, NY, 128 p.

STEIMLE, F. W., C. J. BYRNE, R. N. REID, AND T. R. AZAROVITZ.
1976. Hydrology, sediments, macrofauna and demersal finfish of an alternate disposal site (East Hole in Block Island Sound) for the Thames River (Conn.) dredging project. Final Rep. to U.S. Navy, New London, CT, Informal Rep. #110, 63 p. NOAA, NMFS, MACFC, Sandy Hook Laboratory, Highlands, NJ.

THOMPSON, I., D. S. JONES, AND D. DREIBELBIS.
1980. Annual internal growth banding and life history of the ocean quahog *Arctica islandica* (Mollusca:Bivalvia). Mar. Biol. (Berl.) 57:25-34.

WARNER, J. S.
1976. Determination of aliphatic and aromatic hydrocarbons in marine organisms. Anal. Chem. 48:578-583.

WEAVER, G.
1982. Status report on PCB pollution in New Bedford, Massachusetts. Mass. Executive Off. Environ. Aff., Boston, MA, 69 p.

WENZLOFF, D. R., R. A. GREIG, A. S. MERRILL, AND J. W. ROPES.
1979. A survey of heavy metals in the surf clam, *Spisula solidissima*, and the ocean quahog, *Arctica islandica*, of the Mid-Atlantic coast of the United States. Fish. Bull., U.S. 77:280-285.

AN ECOLOGICAL SURVEY AND COMPARISON OF BOTTOM FISH RESOURCE ASSESSMENTS (SUBMERSIBLE VERSUS HANDLINE FISHING) AT JOHNSTON ATOLL

STEPHEN RALSTON,[1] REGINALD M. GOODING,[1] AND GERALD M. LUDWIG[2]

ABSTRACT

The deep slope (100-365 m) environment at Johnson Atoll in the central Pacific was surveyed with a submersible and the standing crop of commercially important bottom fishes (i.e., lutjanids, serranids, and carangids) estimated by visual quadrat censusing. Results are compared with an assessment made by hook-and-line fishing.

Overall, 69 species of fish were recorded from the submersible and 10 from fishing. Well over half of the sightings from the submersible were new locality records. Bottom fish abundance estimates (fish/hectare and fish/line-hour) varied by site but agreed broadly with one another. Together they are used to estimate catchability (0.0215 hectare/line-hour), which is shown to vary through the day.

Bottom fish were contagiously dispersed along both vertical and horizontal dimensions, with increased numbers of the snapper *Pristipomoides filamentosus* in upcurrent localities. On a finer scale this species and *Etelis coruscans* were aggregated near underwater promontories and headlands, but at different depths.

Numerous observations concerning the deep slope environment of this central Pacific Ocean atoll are included.

Perhaps the most widespread precept in fisheries today is the supposition that catch rate is proportional to stock abundance (Gulland 1974; Ricker 1975; Pitcher and Hart 1982). Even so, there are numerous studies which demonstrate exceptions to this assumption (see for example MacCall 1976; Bannerot and Austin 1983). A departure from linearity in the relationship of these two variables reflects varying catchability. This variation may be due to schooling behavior, gear saturation, or any number of other factors which affect catch per unit effort (CPUE) in addition to stock abundance (Rothschild 1977). It is often difficult, if not impossible, to evaluate the validity of the linearity assumption in most practical situations. A multiple approach to stock assessment has often been suggested as a means of circumventing this problem, including the use of hydroacoustics (Barans and Holliday 1983; Thorne 1983), underwater television-diver surveys (Powles and Barans 1980), and submersibles (Uzmann et al. 1977) to corroborate CPUE data. Consistency in results among a set of independent assessment techniques is necessary for validation and verification of data.

Submersibles in particular have also proven useful in studying the distribution of fishes in various deepwater habitats (Brock and Chamberlain 1968; Strasburg et al. 1968; Colin 1974; Shipp and Hopkins 1978), in identifying nursery grounds of commercially important rockfish species (Carlson and Straty 1981), and in assessing the effectiveness of baited longline gear (High 1980; Grimes et al. 1982). In many situations submersibles provide an ideal means of independent assessment (Uzmann et al. 1977) if questions concerning bias in visual surveys can be adequately addressed (Colton and Alevizon 1981; Sale and Douglas 1981; Brock 1982).

The purpose of this study was to examine the distribution and abundance of tropical deep slope bottom fishes (i.e., lutjanids, serranids, and carangids) at Johnston Atoll in the central Pacific Ocean with a research submersible and to compare the results with an assessment made by fishing. This comparison provides not only a basis for testing the validity of a CPUE statistic, but also for estimating the catchability coefficient. Both are important issues because of the widespread use of hook-and-line catch and effort statistics in resource assessments of bottom fish stocks worldwide (Moffitt 1980; Ralston 1980; Ivo and Hanson 1982; Ralston and Polovina 1982; Munro 1983; Forster 1984). Of special interest was determining the relationship between CPUE and visual estimates of bottom fish standing stock.

[1]Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.
[2]U.S. Fish and Wildlife Service, Honolulu, HI 96850; present address: Florida Fishery Research Station, U.S. Fish and Wildlife Service, P.O. Box 1669, Homestead, FL 33030.

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In addition, a variety of observations made from the submersible substantially improved our understanding of factors controlling the distribution and abundance of the entire deep slope fauna at Johnston Atoll.

DESCRIPTION OF THE STUDY AREA

A National Wildlife Refuge since 1926, Johnston Atoll is located 1,250 km southwest of Oahu, HI. The atoll's physical environment has been reviewed by Amerson and Shelton (1976) and is summarized here.

Located between lat. 16°40′-16°47′N and long. 169°24′-169°34′W (Fig. 1), Johnston Atoll lies in the North Pacific central water mass, where salinities range from 34.8 to 35.3‰. Surface water temperatures show little seasonality, ranging from 25° to 27°C. The atoll is directly in the path of the westerly flowing North Equatorial Current, with surface currents typically 0.5 kn (0.25 m/s). Deeper layers flow smoothly past the atoll, but an island wake forms in lee surface waters, with effects evident up to 600 km downstream (Barkley 1972).

The atoll is composed of a coral platform, encompassing over 130 km^2 of reef under water <30 m deep. A narrow lagoon lies between the northwest barrier reef and Johnston and Sand Islands to the southeast (Fig. 1). The atoll is unusual in that the main outer reef extends only about one quarter of the way around its perimeter (Fig. 1). A large portion of the atoll lies exposed to prevailing easterly weather conditions without benefit of barrier reef protection. Evidence suggests that subsidence and tilting of the reef platform to the southeast created this unusual condition.

The climate is tropical marine, i.e., there is little seasonal variation in temperature and windspeed, but substantial variation in rainfall. A 4-mo "winter" season extends from December to March, when temperatures drop slightly, winds become more variable, and precipitation increases. The mean annual air temperature is 26.3°C, with a daily range of 4.0°-4.5°C. Daily maximum and minimum temper-

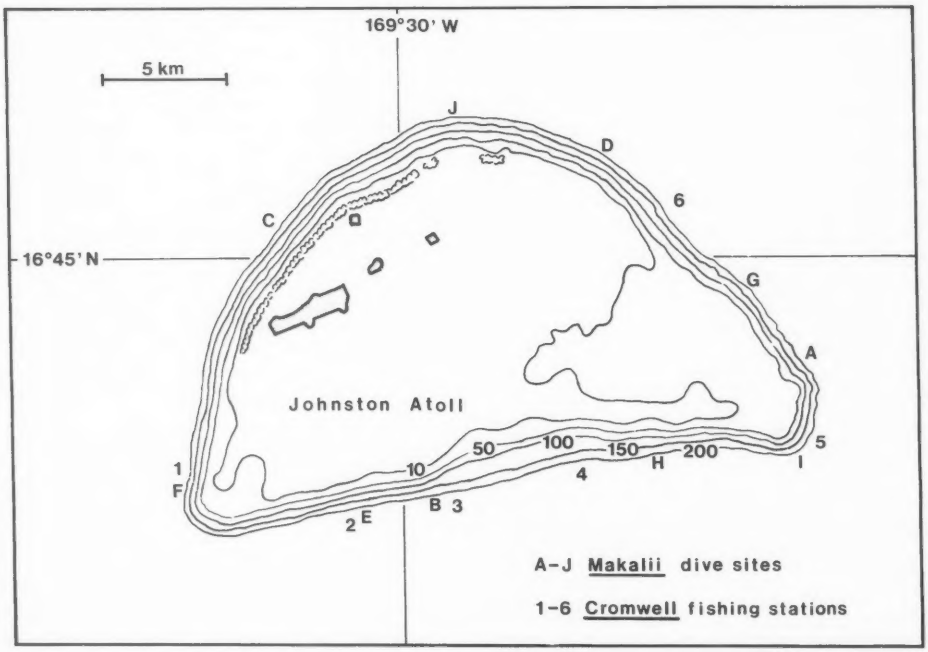


FIGURE 1.—Map of Johnston Atoll. The lines encircling the atoll are isobaths of constant depth (fathoms). The four shaded areas at the upper left are emergent lands (Johnston, Akau, Hikina, and Sand Islands). Letters (A-J) indicate the 10 dive sites of the *Makalii* during the study. Numbers (1-6) indicate fishing stations of the *Townsend Cromwell*.

atures vary little throughout the year, as do sea surface temperatures, which are in near equilibrium with the air. Strong easterly trade winds prevail all year but increase during the summer period. Annual mean wind speed at Johnston Island is 13 kn (7.5 m/s) and monthly means range from 11 to 14 kn (5.5-7.0 m/s).

METHODS

Makalii

The *Makalii* is operated by the National Undersea Research Laboratory at the University of Hawaii. It is a two-man, battery powered, 1-atmosphere submersible which is 4.8 m long, with a pressurized capsule 1.5 m in diameter. When carrying a pilot and one observer, its normal operating speeds range from 1 to 3 kn (0.5-1.5 m/s). Maximum dive duration is 4-5 h and depth capability is 365 m. Equipment carried in this study included hydraulic manipulator, internal and external color video cameras, 2 video monitors, video recorder, video flood lights, Photosea[3] 35 mm still camera with strobe, current and temperature meters, and a dictaphone tape recorder. In addition, the *Makalii* is equipped with an environmental monitoring system for continuous recording of temperature, salinity, conductivity, oxygen, solar radiation, and depth.

All three authors participated as observers during a series of dives at Johnston Atoll over the 2-wk period between 22 September and 5 October 1983. Once on station, a launch-recovery-transport platform was submerged to 20 m and divers released the *Makalii*, usually in 120 m of water. The submersible descended until encountering the bottom and locating the atoll's shelf break. Observations made on fishes during the dives were voice and video recorded for later analysis. Slope angle was periodically measured with a hand-held inclinometer.

Visual estimates of the density of commercially important bottom fishes (sensu Ralston and Polovina 1982) were made by a series of "quadrat" samples. These fishes included *Cookeolus boops*, *Epinephelus quernus*, *Aphareus furcatus*, *A. rutilans*, *Etelis carbunculus*, *E. coruscans*, *Pristipomoides auricilla*, *P. filamentosus*, *P. zonatus*, *Carangoides orthogrammus*, *Caranx lugubris*, *Seriola dumerili*, and *Pontinus macrocephalus*.

During quadrat sampling the observer would look out his port and count the total number of bottom fish, without regard to species, over an area of the bottom judged to be 30 m^2. Quadrat areas always lay on the oblique planar surface of the slope face and were away from the immediate vicinity of the submersible. A sampling period consisted of four counts systematically performed, one every 15 s. To the extent possible, each count was made at an instant in time. All bottom fish seen in the water column above the sample area were included in counts.

The submersible progressed stepwise down the slope (100-365 m) in a clockwise direction around the atoll, with the observer's starboard port always oriented to the slope face. Upon reaching the *Makalii*'s depth limit, a slow stepwise ascent would begin to 100 m, where the dive would end. Descents generally lasted 2.5 h and ascents 1.5 h. Thus the entire vertical distribution of the deep slope was sampled more or less equally (i.e., observations were not concentrated in any particular depth zone).

Townsend Cromwell

The National Oceanic and Atmospheric Administration's (NOAA) RV *Townsend Cromwell* is 50 m long and when rigged for bottom handline fishing carries four hydraulic fishing gurdies (Charlin motors and Pacific King fishing reels), each with 365 m of braided prestretched 90 kg Dacron line. The terminal rig is composed of four No. 28 Tonkichi round fishing hooks and a 2 kg weight. Stripped squid was used for bait and fishing was conducted only during the day.

The vessel spent 3 d (3-5 November 1983) at Johnston Atoll sampling deep slope bottom fish by drift fishing. After wind and current directions had been determined, the vessel was positioned over the desired depth and fishing lines were dropped. Fishing continued until the vessel drifted over an unsuitable water depth, when lines were retrieved and the *Townsend Cromwell* repositioned. Single drifts were the fundamental sampling unit by which catch and effort statistics were summarized. Six fishing stations were occupied (Fig. 1), one during the morning and afternoon of each day. Fork length to the nearest millimeter and depth of capture were recorded for all fish landed.

RESULTS

Makalii

Ten dives were completed at Johnston Atoll (Fig. 1). Due to precipitous dropoffs which occur through-

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

out the study area (100-365 m), the length of the atoll's 183 m (100 fathom) isobath (64 km) provides a convenient measure of total deep slope habitat (Ralston and Polovina 1982). The average point-to-point distance covered by the submersible during one 4-h dive was 2.27 km (s = 0.56 km). An aggregate 22.7 km were thus surveyed during this study, comprising 35% of the deep slope habitat at the atoll.

Temperature

Ambient temperature and depth were recorded often during dives, from which temperature-depth profiles were later constructed. The results are summarized in Figure 2. The solid line represents median temperatures at depth, with the shaded area encompassing the range of temperatures observed among all 10 dives. Surface water temperature was typically 27°C and the mixed layer 100 m deep. A second weak thermocline was found around 240 m. Although its depth varied somewhat (220-245 m), it was present around the entire atoll, i.e., both windward and leeward exposures, and was observed as a shimmering layer below the submersible as it descended. This effect is believed due to refraction of light passing through variable density water, a result of the thermocline in association with a decrease in salinity.[4] Ambient water temperature usually had dropped to 8.5°C at a depth of 350 m.

Slope Angle

The relationship between the bottom's slope and depth was also measured. These data were summarized after each dive and bottom contours plotted. Overall, there was little variation in slope angle around the atoll, i.e., the general pattern was one of uniformity at all sites visited. Figure 3 presents pooled results for all slope angle-depth determinations. In the figure, horizontal and vertical scales are equal and the composite contour of the bottom (100-365 m) at Johnston Atoll is shown in profile. The slope was stratified into three 50-fathom depth zones for later analysis.[5] The slope angle between 50 and 100 fathoms averages $\Theta_1 = 25°$ (Table 1). Similarly, $\Theta_2 = 47°$ and $\Theta_3 = 59°$. There is a definite trend at Johnston Atoll for the slope to steepen with increasing depth, at least between 100 and 365 m.

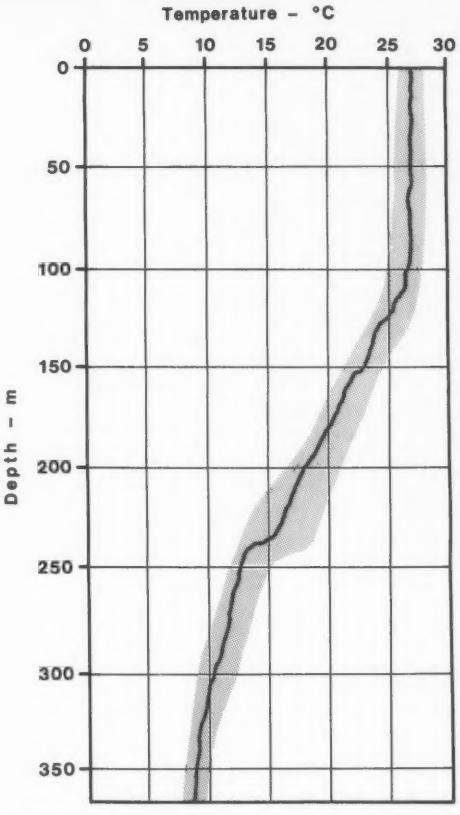


FIGURE 2.—The pooled relationship (n = 10) between temperature and water depth at Johnston Atoll. Solid line = median values; shaded area = range of values.

TABLE 1.—Total habitat areas stratified by depth zones at Johnston Atoll.

Depth stratum (fathoms)	Digitized horizontal planar areas (ha)	Slope angle	Oblique planar habitat areas (ha)
Emergent lands	305 (1%)	—	—
0-10	15,012 (60%)	—	—
10-50	6,123 (24%)	—	—
50-100	1,624 (7%)	25°	1,785
100-150	964 (4%)	47°	1,418
150-200	1,020 (4%)	59°	1,962
Total	25,048 (100%)	—	5,165

In the shallowest regions surveyed (<125 m) the bottom was a monotonous sandy plain in the shoreward direction, but at 125 m it began to slope steeply

[4]E. Chave, Hawaii Undersea Research Laboratory, University of Hawaii, Honolulu, HI 96822, pers. commun. June 1984.

[5]Stratification of depth into zones was performed using units of fathoms (1 fathom = 1.83 m) because nautical charts, hydrographic surveys, and fathometers are so measured. For the sake of brevity and clarity, isobaths and depth strata will henceforth be given only in this unit of measure.

downward. Although not easily seen in the figure, a small but prominant ledge 5-10 m high encircled the atoll between 130 and 140 m. Somewhat deeper, between 180 and 275 m, the bottom was uniform in slope and its surface relatively smooth and devoid of features. Slope angles approached the vertical at most sites in the 300-350 m depth range, with overhanging caves formed by subaerial dissolution.[6] At the deepest points visited (360 m) the bottom became less precipitous, and in some areas a sediment-laden terrace had formed along the base of the deep dropoff.

Based on estimates of slope angle, existing charts, and a hydrographic survey by the *Townsend Cromwell*, habitat areas for the three depth zones were determined. The positions of the 10 and 100-fathom isobaths were already known, but they were refined and the locations of the 50-, 150-, and 200-fathom isobaths estimated. Figure 1 is a simplified representation of a much larger chart which was digitally analyzed to determine the horizontal (i.e., level) areas bounded by isobaths (Table 1). The results show that emergent lands (Johnston, Akau, Hikina, and Sand Islands) account for only 1% (305 ha) of the level planar area of the atoll. The largest area (60%) lies between sea level and 10 fathoms. The total horizontal extent of the atoll is about 25,000 ha.

These results can be misleading, however, because a vertical slope provides no horizontal habitat area, and yet both reef fish diversity and standing crop are known to be positively correlated with topographic relief (Luckhurst and Luckhurst 1978; Gladfelter et al. 1980; Carpenter et al. 1981). At Johnston Atoll the structural complexity of the substratum frequently increased with slope angle. A better estimate of total habitat is the area of bottom irrespective of slope angle, estimated by dividing the horizontal planar area of a depth stratum by the cosine of the slope angle within it. This adjustment almost doubles the estimate of total habitat area in the 150-200 fathom zone, simply due to the precipitous dropoff found there. A composite 5,165 ha of habitat occurs between 50 and 200 fathoms.

General Observations

While this study focused primarily on the deepwater ichthyofauna of Johnston Atoll, many observations were made on the oceanographic, geologic, and biotic characteristics of the study area. These are briefly recounted here.

Currents running in directions parallel to the slope were frequently encountered. They were generally weak and did not exceed 0.3 kn (0.15 m/s). They sometimes exhibited reversals with depth. During

[6]Keating, B. H. Geologic history and evolution of Johnston Island: Submersible dive results. Manuscr. in prep. University of Hawaii, Honolulu, HI 96822.

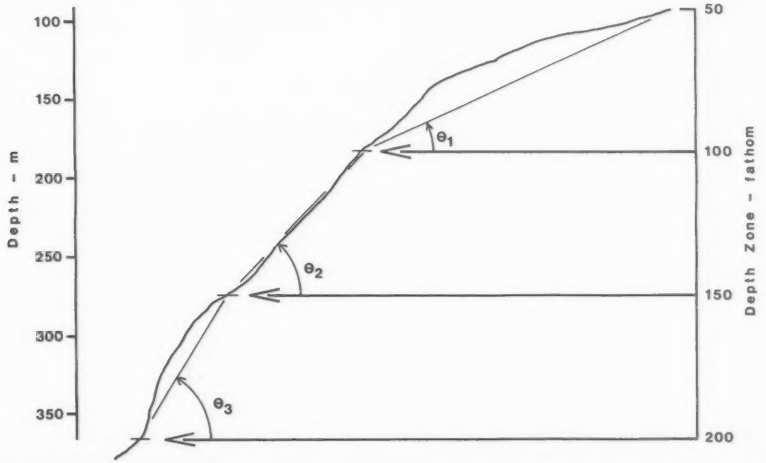


FIGURE 3.—Composite reconstruction of the deep slope at Johnston Atoll. Horizontal and vertical scales equal. Average slope angles (θ) were measured for each of three 50-fathom depth strata.

dive F, for example (Fig. 1), a 0.2 kn (0.10 m/s) current was observed at 125 m running south (i.e., counterclockwise when viewed from above). There was no current between 180 and 275 m. At 300 m, however, a 0.1 kn (0.05 m/s) current was observed, traveling in a northerly direction (i.e., clockwise). A similar depth-related current reversal was observed during dive C, although on this occasion the shallower current (170 m) ran clockwise and the deeper one (290 m) counterclockwise. In contrast, a weak downslope current (0.1 kn or 0.05 m/s) was observed but once (dive E at 305 m). No upwelling currents were encountered.

Geologically, the deep slope of Johnston Atoll was grossly similar at all points visited. The low escarpment at 130 m was most likely due to erosion of an ancient limestone reef. This feature was characterized by mounds of coral rubble, boulders, small undercut caves, and a profusion of fishes. Below it the slope angle was remarkably uniform, with low topographic relief. The bottom was still composed of limestone and showed severe biological and chemical weathering (i.e., dissolution) along the slope gradient, being pitted and striated with numerous shallow depressions. Few sediments or boulders were observed. At a depth of 240 m topographic relief increased, as large slab boulders became increasingly prominent. Subaerial dissolution had produced low shallow limestone caves, and fine sediments were more common. Between 290 and 335 m the slope was very steep, with a well-developed system of sharp ridges and deep erosional channels. The substratum had the superficial appearance of dark basalt but was composed of thin manganese crusts overlying ancient limestone reef materials (Keating see footnote 6). Fine sediments spilled down the channels in the slope and piled up at the base of the deep dropoff (350 m). More limestone boulders were arrayed along this deep terrace and fine sediments covered the bottom.

As expected, few fleshy macroalgae were seen. The only algae encountered regularly were two corallines, *Halimeda* sp. and an unidentified crustose species. The former occurred in small scattered clumps between 100 and 200 m, with loose remnant exoskeletal "sands" found in sediment pockets as deep as 290 m. The crustose form was abundant between 150 and 250 m where it covered much of the slope face. Otherwise, an unidentified species of brown algae seen on dive H between 150 and 250 m was the only other algae seen. A more detailed description of the algal biota at Johnston Atoll is in preparation.[7]

In contrast to the depauperate flora, the invertebrate fauna was rich. Listed here are those forms seen often enough to constitute indicator species for particular depth strata. In addition to these a great many others were observed and photographed. In the Cnidaria, three stoney corals were especially plentiful: *Leptoseris hawaiiensis* (115-165 m), *Stylaster* sp. (135-245 m), and *Madracis* sp. (140-200 m). Several species of black corals (Order Antipatharia) were also common. Of the crustaceans, a single large *Panulirus marginatus*, previously known only from one specimen (Brock 1973), was observed in a small hole during dive A at 122 m, and at least two types of galatheid crab were very abundant in small holes pitting the reef slope between 230 and 350 m. In deep water the remaining attached valves of dead rock oysters were seen in patches along the base of the deep dropoff (350 m), as was an unidentified species of solitary tunicate (335-365 m). Echinoids were particularly abundant immediately below the shelf break; e.g., *Diadema* cf. *savignyi* (110-170 m), *Chondrocidaris gigantea* (120-160 m), and heart urchins (Brissidae, 130-200 m). Other than galatheid crabs, the 220-310 m zone was largely barren and devoid of megabenthos.

Ichthyofauna

A total of 69 fish species in 29 families were observed during *Makalii* dives (Table 2). Overall, the proportional representation of different families was similar to that of the shallow water community (Gosline 1955; Randall et al. in press), although the representation of genera was grossly different. Serranid species were most numerous with nine species observed (eight in the anthiine subfamily). Lutjanids were also abundant (eight species), but no members of the ubiquitous genus *Lutjanus* were seen. Forty of the species listed in Table 2 (58%) are new records for Johnston Atoll (Randall et al. in press). Photographs of several fishes observed during dives are presented in Figure 4.

An indication of species' depth distributions is given in Table 2. Because no observations were made in <100 m, upper limits can be misleading. This is particularly true of shallow-water species which penetrated to the 135 m escarpment but not beyond, including: *Triaenodon obesus*, *Parapercis schauinslandi*, *Aphareus furcatus*, *Chromis verater*, *Parupeneus cyclostomus*, *P. multifasciatus*, *Forcipiger flavissimus*, *Holacanthus arcuatus*, *Bodianus bilu-*

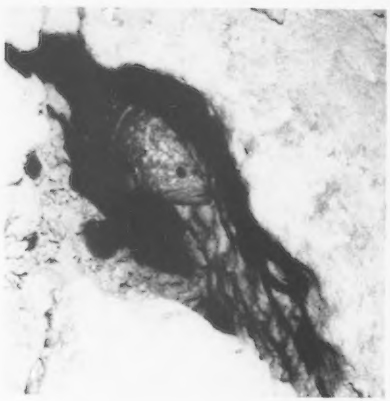
[7]C. Agegian, University of Hawaii, Honolulu, HI 96822, pers. commun. June 1984.

TABLE 2.—Fishes encountered during dives (100-365 m) of the *Makalii* at Johnston Atoll. Included for each species are the minimum and maximum depths (m) of observation as well as the median and range of the depth distribution. Under the sighting column a value of 1 indicates a species was seen repeatedly (>5 times) during each dive of the submersible, 2 means the species was occasionally seen on each dive (<5 times), 3 signifies sightings on most dives but not all (i.e., species seen on several occasions), and 4 indicates rarity (see only once or twice during all dives). An asterisk to the left of a species name signifies a new record for Johnston Atoll (Randall et al. in press).

Family-species	Min-max	Median (range)	Sighting
Carcharhinidae			
Carcharhinus amblyrhynchos	90-275	185(185)	1
Carcharhinus sp. (probably *galapagensis*)	225-250	225(25)	3
Triaenodon obesus		120	4
Mobulidae			
Manta sp.		120	4
Muraenidae			
**Gymnothorax berndti*	220-260	260(40)	3
**G. nudivomer*	120-205	179(85)	2
**G. nuttingi*	185-300	250(115)	3
Ophichthidae			
Myrichthys maculosus	150-215	185(65)	4
Synodontidae			
Unidentified synodontid		240	4
Holocentridae			
**Myripristis chryseres*	135-240	155(105)	2
**Neoniphon aurolineatus*		150	4
**Pristilepis oligolepis*	165-345	230(180)	3
Ophidiidae			
Brotula sp. (*multibarbata* or *townsendi*)		230	4
Priacanthidae			
**Cookeolus boops*	165-260	220(95)	1
Serranidae			
**Anthias fuscinus*	135-280	215(145)	1
**A. ventralis*		105	4
Callanthias sp.	240-330	285(90)	4
**Epinephelus quernus*	135-350	230(215)	1
**Grammatonotus laysanus*	310-350	335(40)	3
**Holanthias elizabethae*	155-260	230(105)	1
**H. fuscipinnis*	160-215	170(55)	1
Luzonichthys sp. (perhaps *earlei*)		105	4
**Plectranthias helenae*	215-220	215(5)	3
Mugiloididae			
**Parapercis roseoviridis*	215-270	245(55)	2
**P. schauinslandi*	105-170	145(65)	1
Lutjanidae			
Aphareus furcatus	105-145	135(40)	2
**A. rutilans*	190-250	220(60)	3
**Etelis carbunculus*	245-365	310(120)	3
**E. coruscans*	250-355	270(105)	3
**Pristipomoides auricilla*	215-250	230(35)	3
**P. filamentosus*	120-260	205(140)	3
**P. zonatus*	205-295	240(90)	1
**Symphysanodon maunaloae*	230-365	300(135)	1
Emmelichthyidae			
**Erythrocles scintillans*	295-320	300(25)	4
Carangidae			
Carangoides orthogrammus	105-170	135(65)	2
Caranx lugubris	105-355	190(250)	1
C. melampygus	130-230	135(100)	2
Decapterus sp.		100	4
**Elagatis bipinnulata*	90-150	120(60)	3
**Seriola dumerili*	120-335	215(215)	1
Apogonidae			
**Epigonus* sp.	330-365	355(35)	2
Pomacentridae			
Chromis verater	120-140	130(20)	3
Mullidae			
Parupeneus cyclostomus		125	4
P. multifasciatus		125	4
Chaetodontidae			
**Chaetodon modestus*	125-255	190(130)	2
**C. tinkeri*	105-160	145(55)	3
Forcipiger flavissimus	125-145	130(20)	4
**Heniochus diphreutes*	120-215	135(95)	2
Pomacanthidae			
Geniacanthus sp.		150	4
**Holacanthus arcuatus*	130-150	135(20)	3
Labridae			
Bodianus bilunulatus	130-135	130(5)	3
Cheilinus unifasciatus		120	4
**Polylepion russelli*	245-280	275(35)	3
Acanthuridae			
**Acanthurus dussumieri*		130	4
**Naso hexacanthus*	120-165	150(45)	2
**Naso* sp.	120-175	135(55)	1
Zanclidae			
Zanclus cornutus		125	4
Scorpaenidae			
**Pontinus macrocephalus*	200-365	305(165)	2
**Scorpaena colorata*		272	4
Scorpaena sp.	225-355	290(130)	2
Triglidae			
**Satyrichthys engyceros*	355-365	365(10)	4
Bothidae			
Bothus mancus	270-350	310(80)	4
Balistidae			
**Sufflamen fraenatus*	105-170	140(65)	1
Xanthichthys auromarginatus	115-155	135(40)	1
Monacanthidae			
Unidentified monacanthid		125	4
Tetraodontidae			
**Canthigaster* sp. (likely *inframacula*)	260-270	265(10)	4
Unidentified tetraodontid	135-150	145(15)	4
Ostraciidae			
Ostracion sp.		135	4
Diodontidae			
Diodon hystrix		135	4

nulatus, *Acanthurus dussumieri*, *Zanclus cornutus*, *Xanthichthys auromarginatus*, and *Diodon hystrix*. These fishes accounted for an increase in diversity at the 135 m dropoff. Similarly, due to the submersible's 365 m depth limit, lower bounds for some species are likely in error (e.g., *Symphysanodon maunaloae*, *Epigonus* sp., *Pontinus macrocephalus*, and *Satyrichthys engyceros*). Nonetheless, due to the large depth range sampled (100-365 m), the data still provide useful estimates of the depth distributions for most of the species listed.

The data suggest that large species have great



depth ranges. For example, all species with depth ranges exceeding 200 m are large (i.e., *Caranx lugubris*, *Epinephelus quernus*, and *Seriola dumerili*). Moreover, among extensively observed species, a significant Spearman correlation exists between ranked average weight and depth range (r_s = 0.52, df = 25, $P < 0.01$). This finding should be viewed with caution because of potential biases in depth distributions (see above).

The last column in Table 2 gives sighting scores for all species. Those assigned a value of 1 indicate species dominating the deep slope fish community in terms of species sightings. Note that some species were seen infrequently, but when encountered they were observed in large numbers (e.g., *Elagatis bipinnulata*, Fig. 4). Similarly, *Pristipomoides filamentosus* was not seen on every dive and was thus assigned an abundance score of 3. In spite of this, when seen, it was abundant and it was the most frequently caught while fishing (see next section). Sighting scores therefore do not indicate relative species' contributions to total standing crop biomass of the deep slope fish fauna.

Quadrat Sampling

A total of 974 quadrat sample counts were made during the 10 submersible dives. No attempt was made to estimate abundance separately for each species. Rather, the total number of bottom fish was recorded, regardless of species composition. Although severely reducing the detail of the data base, this did have the desirable effect of averaging biases due to attraction or repulsion of fishes to and from the *Makalii*. It was evident, for example, that some species were attracted to the submersible and followed it about (e.g., *Seriola dumerili* and *Caranx lugubris*), whereas others were repelled and actively avoided the submersible's lights (e.g., *Pristipomoides filamentosus* and *Etelis coruscans*). Still others did not seem to be greatly influenced (e.g., *Cookeolus boops*, *Epinephelus quernus*, *Pristipomoides zonatus*, and *Pontinus macrocephalus*). By pooling species quadrat counts, the abundance of some species was overestimated, some underestimated, and some estimated without bias. Due to averaging, we believe that pooled counts provide the best available estimates of total bottom fish density along the deep slope of Johnston Atoll.

Some 367 bottom fish were counted in quadrat samples, resulting in a mean encounter rate of 0.38 fish/quadrat. The data were fitted to the Poisson distribution to ascertain the dispersion pattern. A chi-square goodness of fit test yielded χ^2 = 325.32, df = 3, $P << 0.005$, demonstrating nonrandom dispersion. The variance to mean ratio calculated from the frequency distribution of bottom fish/quadrat observations was 4.64 and was significantly greater than 1 ($P << 0.005$), indicating strong contagion.

One of the principal explanations for this result is shoaling by *Pristipomoides filamentosus* and *Etelis coruscans*. Both are large species, which formed aggregations of up to 100 individuals well off the bottom (20 m) in the vicinity of underwater headlands and promontories. These monospecific groups appeared to feed in open water on plankton, consistent with previous dietary studies of *P. filamentosus* (Kami 1973; Ralston[8]). When either was observed, there was an increased likelihood of encountering conspecifics. As a consequence 10 or more *P. filamentosus* were seen in one quadrat on 7 occasions.

Another factor contributing to clumping was nonrandom distribution with depth (Fig. 5). This figure presents the relationship between mean number of bottom fish per count and depth (vertical bars = standard errors). Note the two abundance peaks, the first at about 170 m and the second at 250 m. The former was due primarily to large numbers of *Caranx lugubris* and *P. filamentosus*. The location of the second peak was just below the second thermocline and was largely the result of local increases in numbers of *Epinephelus quernus* and *P. zonatus*.

The mean numbers of bottom fish per quadrat, stratified into 50-fathom depth intervals, are also shown in Figure 5 (i.e., 0.57, 0.47, and 0.06 fish/count). These data were converted to densities (1 quadrat = 0.003 ha) such that from 50 to 100 fathoms an average of 190 bottom fish are estimated to occur per hectare of habitat. Similarly, in the two deeper strata, estimated densities of 156 and 20 bottom fish/ha occur.

Given estimates of bottom fish density and depth-specific estimates of total available habitat (Table 1), estimates of the total standing crop of bottom fishes at Johnston Atoll indicate that about 339,000 fish occurred in the 50-100 fathom zone, 221,000 between

FIGURE 4.—Johnston Atoll deep slope fishes. A. *Caranx lugubris* with wire coral; B. *Epinephelus quernus* peering out of cave; C. *Seriola dumerili* (foreground) and *Caranx lugubris* (background); D. school of *Elagatis bipinnulata* with *Carangoides orthogrammus* (above); E. *Heniochus diphreutes* with black coral; and F. aggregation of *Myripristis chryseres* and *Neoniphon aurolineatus*.

[8]Ralston, S. Unpubl. data. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

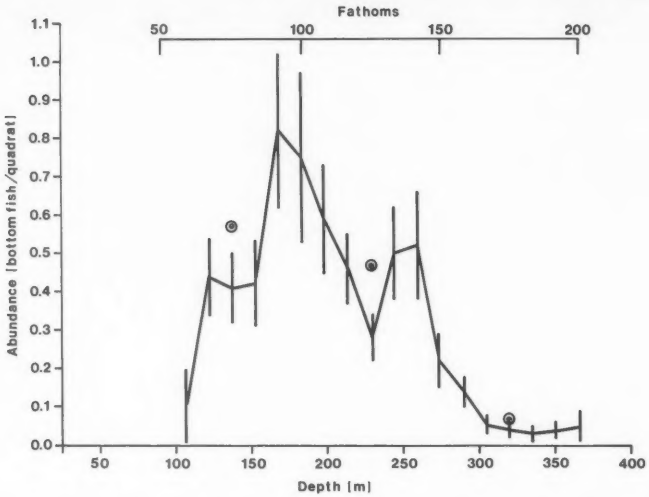


FIGURE 5.—The abundance of bottom fish (see text) in relation to depth. Solid line represents fish densities with changing depth (measured in meters or fathoms). Error bars are standard errors of means. Three 50-fathom depth zones are indicated, and mean fish densities within these are shown as circled points.

100 and 150 fathoms, and only 39,000 in the deepest (150-200 fathom) zone. Roughly 600,000 commercially exploitable bottom fish are estimated to comprise the deep-sea hook-and-line resource at Johnston Atoll. Because the fish are spread over a total habitat of 5,165 ha (Table 1), this corresponds to average densities of 118 bottom fish/ha.

Townsend Cromwell

Anywhere from 2 to 4 lines were deployed while fishing, resulting in an aggregate 41.8 line-h of fishing effort spread over 23 vessel drifts. A catch of 133 fishes (Table 3) produced an overall CPUE of 3.18 fish/line-h. Another 12 fish were hooked but lost to sharks before landing. All species caught while fishing were observed from the submersible with the exception of the bramid, *Eumegistus illustris*. Deepwater lutjanids predominated (69%), but substantial numbers of serranids (22%) and carangids (8%) were caught, a composition typical of tropical deep slope fisheries worldwide (Talbot 1960; Ralston and Polovina 1982; Munro 1983; Forster 1984).

Species Composition By Location

Examination of catch data suggested a difference in species composition between upcurrent (sites 5 and 6) and downcurrent (sites 1-4) locations (Fig. 1). Landings were pooled into these two classes, and also by species category into *Pristipomoides filamentosus*, *P. zonatus*, *Epinephelus quernus*, and "others". The resulting 2 × 4 contingency table showed a lack of statistical independence between locations and species (χ^2 = 22.36, df = 3, $P << 0.005$). Examin-

TABLE 3.—Species composition of the bottom fish catch from the *Townsend Cromwell* at Johnston Atoll.

Family-species	Catch (*n*)	Percent	Average size (cm FL)
Lutjanidae (snappers)			
Pristipomoides filamentosus	43	32	54.4
P. zonatus	35	26	40.8
P. auricilla	5	4	34.6
Etelis carbunculus	5	4	51.2
E. coruscans	4	3	72.7
Subtotal	92	69	
Serranidae (groupers)			
Epinephelus quernus	29	22	69.8
Carangidae (jacks)			
Caranx lugubris	7	5	48.1
Carangoides orthogrammus	2	2	43.5
Seriola dumerili	2	2	79.5
Subtotal	11	9	
Bramidae (pomfrets)			
Eumegistus illustris	1	1	70.3
Grand total	133	101	

ing individual contingency table cells showed that the greatest contribution to the total chi-square was for *P. filamentosus* (58% of total). Specifically, under the hypothesis of independence, 16.5 were expected downcurrent but only 5 were caught, while 26.5 were expected upcurrent where 38 were landed. The apparent surplus of *P. filamentosus* along the eastern exposure, where trade winds prevail and oceanic currents first impact the atoll (Barkley 1972), may relate to this fish's habit of feeding on large deepwater plankton, especially salps (genus *Pyrosoma*). Bray (1981) has shown that small resident planktivores will travel to the upcurrent edge of a reef to access pelagic plankton. The distribution of *P. filamentosus* at Johnston Atoll may represent a similar situation on a much larger scale.

Bottom Fish Catch Rate

One-way analysis of variance (ANOVA) of CPUE data was used to examine whether geographical differences exist in bottom fish abundance, i.e., the two treatment classes were upcurrent and downcurrent regions (see above). The ANOVA was insignificant ($F = 1.62$, df = 1, 21, $P = 0.21$), although the mean catch rate along the eastern exposure (5.6 bottom fish/line-h) was 60% greater than downcurrent (3.5 bottom fish/line-h). This result suggests the lack of significance may have been due to small sample size.

The CPUE data were analyzed by time of day to determine if catchability fluctuates through the day. The results in Figure 6 show that fishing was distinctly better during the morning than afternoon. In this figure individual values of drift CPUE (n = 23) have been plotted against the midpoint of the drift time interval. The solid line represents aggregate catch rates, calculated by pooling both catch and effort statistics from all areas into 1-h intervals and then forming CPUE ratios. Different symbols represent each of six separate fishing locations (Fig. 1). Note that catch rates were highest when fishing began each day and consistently declined to a low during the midafternoon. The data further indicate that catch rates may increase again with the onset of the evening crepuscular period, although the data are meager. This pattern was evident both within and among the six sites fished and, when averaged out, resulted in morning catch rates 2.07 times greater than afternoon rates.

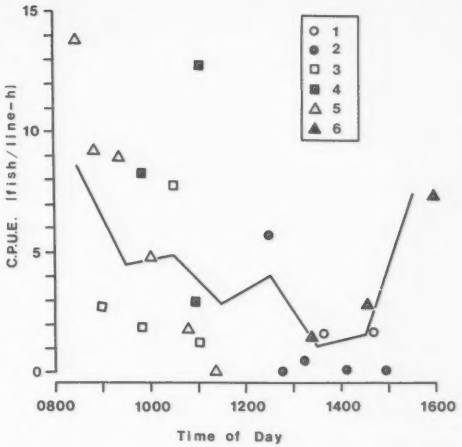


FIGURE 6.—The effect of time of day on the catch rate of bottom fish at Johnston Atoll. Catch rates calculated for each drift of the vessel and presented for each of six different fishing stations (see Figure 1).

Catchability

Having the *Makalii* and *Townsend Cromwell* at Johnston Atoll at similar times prompts comparison of the assessment techniques. We assume that in the 1-mo interim between visits no changes occurred in overall levels of abundance, because Johnston Atoll is a National Wildlife Refuge where no fishing is permitted and the fishes are typically long lived (Ralston and Miyamoto 1983; Ralston see footnote 8). Any differences in assessment are then likely due to differences in method.

To compare surface estimates of bottom fish abundance with those derived from submersible surveys, we matched fishing stations (numbers) with submersible dives (letters) which occurred nearby (Fig. 1). Specific pairings were F-1, E-2, B-3, H-4, I-5, and D-6. For each dive the overall abundance of bottom fish was estimated by forming the ratio of total fish counted to total number of quadrat counts, and then converting to density measured in bottom fish/ha. The CPUE statistics were used to estimate abundance for each fishing station, after correcting for fluctuating catchability (Fig. 6). The result is presented in Figure 7. There is a positive correlation between CPUE and bottom fish density ($r = 0.54$), although it is insignificant.

One means of estimating catchability, q, is to determine the slope of the regression of CPUE on stock density. We estimated the functional regression (Ricker 1973) of the data presented in Figure 7 (solid line) and determined that $q = 0.0215$ ha/line-h. A second estimate of q is obtained by forming the ratio of the average catch rate of bottom fish at the atoll

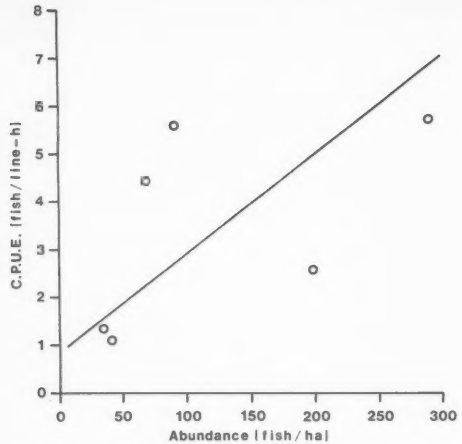


FIGURE 7.–The relationship between *Townsend Cromwell* CPUE and *Makalii* abundance estimates. Line fitted by functional regression. See text for further discussion.

(3.18 fish/line-h) to the average density of bottom fish viewed from the submersible (118 bottom fish/ha). The resulting estimate of q is 0.0269 ha/line-h.

DISCUSSION

The most enlightening aspect of this study was our ability to perform an in situ assessment of factors controlling the distribution and abundance of the deep slope biota at Johnston Atoll. Organisms showed not only distinct zonational patterns with depth but clumped dispersion along horizontal gradients as well.

The fish fauna of Johnston Atoll is often considered a depauperate outlier of the Hawaiian fauna (Gosline 1955; Randall et al. in press). In a later paper, Gosline (1965) examined vertical zonation in Hawaiian fishes, arguing that depth zonation patterns are often sharply demarcated in intertidal and shallow-water habitats, but these become increasingly attenuated with depth. The results of our study and Randall et al. (in press) support his conclusion (see also Forster 1984). Some deep slope species have extremely broad depth ranges (exceeding 200 m), yet few representatives of the shallow-water community extend appreciably beyond the 130 m escarpment encircling the atoll. Other investigators have noted that many Hawaiian species, which are commonly thought of as strictly associated with coral reefs, penetrate to depths well in excess of those favoring the growth of scleractinian corals (Brock and Chamberlain 1968; Strasburg et al. 1968; Clarke 1972). Yet the distributions of these fishes are limited largely to areas near the shelf break or shallower, while a true deep slope ichthyofauna, comprised largely of anthiids and lutjanids, exists along outer reef drop-offs at both Johnston Atoll and in the Hawaiian Islands.

Distributional patterns of fishes were nonrandom along horizontal gradients as well, as was readily apparent in the atoll-wide distribution of *Pristipomoides filamentosus*. Based simply on catch totals, 60% more *P. filamentosus* were expected to occur on the upcurrent exposure of the atoll than downcurrent, although 760% more were observed there, illustrating the clumped dispersion pattern which characterized this species during fishing surveys. Contagion was also evident in quadrat samples. Future studies would be well advised to incorporate statistical models consistent with these findings, including use of the negative binomial distribution to describe spatial patterns.

On a more local scale, it was clear from submersible observations that *P. filamentosus* and *Etelis coruscans* were concentrated near underwater headlands. Brock and Chamberlain (1968) made similar observations on deepwater populations of *Chaetodon miliaris*, attributing the very localized distribution of this species to increased accessibility of its food (plankton) in the vertical turbulence plumes formed by the impact of currents on underwater promontories. Because of its known planktivorous food habits, this hypothesis could explain abundance patterns of *P. filamentosus*. Moreover, fishermen emphasize the importance of currents in locating feeding aggregations of both *P. filamentosus* and *E. coruscans*. These two species taken together comprise the most important species landed in the Hawaiian deep-sea hook-and-line fishery, both in terms of yield and economic value. The relative abundance of these species in the deepwater bottom fish community may be due to their utilization of an allochthonous plankton resource transported to neritic waters from the open sea.

Bottom Fish Abundance

Certain methodological problems hindered this study and should be reviewed before comparing the abundance estimates from the two surveys. Any technique, including those used here, has its own specific combination of advantages and disadvantages.

There is ample reason to suspect bias in assessments based on underwater visual surveys. Sale and Douglas (1981) have shown that a single visual fish

census seldom records all individuals present at the time of the census. Similarly, Colton and Alevizon (1981) showed that a quarter of the community they studied was characterized by significant diurnal changes in abundance. They concluded that unless sampling time is carefully controlled and standardized, results from visual abundance surveys may be seriously biased. Standardization was achieved in this study because all 10 dives started between 0840 and 0950 in the morning and each lasted 4 h. Furthermore, Brock (1982) showed that large, conspicuous, diurnally active species are accurately censused with visual assessment techniques, although the most abundant are often underestimated. With the exception of *Cookeolus boops*, which, although nocturnal, shelters in the open along the slope face, all of the species included in the quadrat sampling fit these criteria. Biases which frequently accompany visual assessments have thus been considered and minimized here.

Another factor which may have affected the results of *Makalii* surveys is attraction and repulsion of certain species to and from the submersible. Previous investigators have typically ignored this problem (Uzmann et al. 1977; High 1980; Powles and Barans 1980; Carlson and Straty 1981), while at the same time acknowledging that some species are attracted (e.g., black sea bass, southern porgy, Pacific halibut, sculpin, and yelloweye rockfish) or repelled (e.g., squid, herring, mackerel, butterfish, and wolf eel) to submersibles and divers. Nevertheless, as pointed out by Uzmann et al. (1977), one can at least observe the reactions of species to the submersible's presence, giving the viewer the opportunity to evaluate potential sources of error. We have attempted to address this problem by pooling counts for all species. While admittedly this procedure may not remove all bias, it is our feeling that in the absence of more quantitative information, little else can be done to improve the data. Studies are now being implemented to specifically evaluate the degree of attraction or repulsion of different species to the *Makalii*.

Provided an awareness of these concerns, the results presented here support the contention that the catch of bottom fish/line-h is a suitable CPUE statistic. This conclusion is based on the data presented in Figure 7, where CPUE generally increases with fish density and the regression intercept passes close to the origin. Although the relationship is statistically insignificant, this is likely due to small sample size ($n = 6$). Moreover, differences in bottom fish abundance between upcurrent and downcurrent locations were shown to result largely from the contagious dispersion of *Pristipomoides filamentosus* along the eastern side of the atoll, where its primary food resource first becomes available for consumption.

The estimation of catchability for deep-sea hook-and-line gear is a useful application of the dual sampling program presented here. The results suggest relatively great sensitivity of bottom fish stocks to exploitation pressure, a finding consistent with previous and ongoing studies (Ralston 1984). If we use $q = 0.0215$ ha/line-h as an estimate of catchability, we conclude that 1 line-h of *Townsend Cromwell* fishing effort removes about 2.2% of the bottom fish inhabiting 1 ha of habitat. A similar finding was reported by Polovina[9], who estimated q from the same vessel for a Mariana stock of bottom fish. Removals such as this are not insubstantial and underscore the importance of developing methods of stock assessment which can be used early in the development of a fishery and in the absence of conventional data sources. A combination of surface platform surveys with submersible ground-truthing is certainly a promising assessment technique to pursue (Uzmann et al. 1977).

ACKNOWLEDGMENTS

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LITERATURE CITED

AMERSON, A. B., JR., AND P. C. SHELTON.
1976. The natural history of Johnston Atoll, central Pacific Ocean. Atoll Res. Bull. 192:1-479.

BANNEROT, S. P., AND C. B. AUSTIN.
1983. Using frequency distributions of catch per unit effort to measure fish-stock abundance. Trans. Am. Fish. Soc. 112:608-617.

BARANS, C. A., AND D. V. HOLLIDAY.
1983. A practical technique for assessing some snapper/grouper stocks. Bull. Mar. Sci. 33:176-181.

BARKLEY, R. A.
1972. Johnston Atoll's wake. J. Mar. Res. 30:201-216.

BRAY, R. N.
1981. Influence of water currents and zooplankton densities

[9]Polovina, J. J. A variable catchability version of the Leslie model with application to an intensive fishing experiment on a multispecies stock. Manuscr. submitted to U.S. Natl. Mar. Fish. Serv., Fish. Bull.

on daily foraging movements of blacksmith, *Chromis punctipinnis*, a planktivorous reef fish. Fish. Bull., U.S. 78:829-841.

BROCK, R. E.
1973. A new distributional record for *Panulirus marginatus* (Quoy & Gaimard, 1825). Crustaceana 25:111-112.
1982. A critique of the visual census method for assessing coral reef fish populations. Bull. Mar. Sci. 32:269-276.

BROCK, V. E., AND T. C. CHAMBERLAIN.
1968. A geological and ecological reconnaissance off western Oahu, Hawaii, principally by means of the research submarine "Asherah." Pac. Sci. 22:373-394.

CARLSON, H. R., AND R. R. STRATY.
1981. Habitat and nursery grounds of Pacific rockfish, *Sebastes* spp., in rocky coastal areas of southeastern Alaska. Mar. Fish. Rev. 43(7):13-19.

CARPENTER, K. E., R. I. MICLAT, V. D. ALBALADEJO, AND V. T. CORPUZ.
1981. The influence of substrate structure on the local abundance and diversity of Philippine reef fishes. *In* E. D. Gomez, C. E. Birkeland, R. W. Buddemeier, R. E. Johannes, J. A. Marsh, Jr., and R. T. Tsuda (editors), The reef and man, p. 497-502. Proceedings of the Fourth International Coral Reef Symposium, Vol. 2. Mar. Sci. Cent., Univ. Philippines, Quezon City.

CLARKE, T. A.
1972. Collections and submarine observations of deep benthic fishes and decapod Crustacea in Hawaii. Pac. Sci. 26:310-317.

COLIN, P. L.
1974. Observation and collection of deep-reef fishes off the coasts of Jamaica and British Honduras (Belize). Mar. Biol. (Berl.) 24:29-38.

COLTON, D. E., AND W. S. ALEVIZON.
1981. Diurnal variability in a fish assemblage of a Bahamian coral reef. Environ. Biol. Fishes 6:341-345.

FORSTER, G. R.
1984. The distribution of fishes on the outer reef slopes of Aldabra (Indian Ocean) in relation to bottom temperatures. Environ. Biol. Fishes 10:129-136.

GLADFELTER, W. B., J. C. OGDEN, AND E. H. GLADFELTER.
1980. Similarity and diversity among coral reef fish communities: A comparison between tropical western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Islands) patch reefs. Ecology 61:1156-1168.

GOSLINE, W. A.
1955. The inshore fish fauna of Johnston Island, a central Pacific atoll. Pac. Sci. 9:442-480.
1965. Vertical zonation of inshore fishes in the upper water layers of the Hawaiian Islands. Ecology 46:823-831.

GRIMES, C. B., K. W. ABLE, AND S. C. TURNER.
1982. Direct observation from a submersible vessel of commercial longlines for tilefish. Trans. Am. Fish. Soc. 111:94-98.

GULLAND, J. A.
1974. The management of marine fisheries. Univ. Washington Press, Seattle, 198 p.

HIGH, W. L.
1980. Bait loss from halibut longline gear observed from a submersible. Mar. Fish. Rev. 42(2):26-29.

IVO, C. T. C., AND A. J. HANSON.
1982. Aspectos da biologia e dinamica populacional do pargo, *Lutjanus purpureus* Poey, no norte e nordeste do Brasil. Arq. Cienc. Mar 22(1/2):1-41.

KAMI, H. T.
1973. The *Pristipomoides* (Pisces: Lutjanidae) of Guam with notes on their biology. Micronesica 9:97-118.

LUCKHURST, B. E., AND K. LUCKHURST.
1978. Analysis of the influence of substrate variables on coral reef fish communities. Mar. Biol. (Berl.) 49:317-323.

MACCALL, A. D.
1976. Density dependence of catchability coefficient in the California Pacific sardine, *Sardinops sagax caerula*, purse seine fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 18:136-148.

MOFFITT, R. B.
1980. A preliminary report on bottomfishing in the Northwestern Hawaiian Islands. *In* R. W. Grigg and R. T. Pfund (editors), Proceedings of the Symposium on Status of Resource Investigations in the Northwestern Hawaiian Islands, April 24-25, 1980, University of Hawaii, Honolulu, Hawaii, p. 216-225. Sea Grant Misc. Rep. UNIHI-SEAGRANT-MR-80-04.

MUNRO, J. L. (editor).
1983. Caribbean coral reef fishery resources. ICLARM Studies and Reviews 7, Manila, 276 p.

PITCHER, T. J., AND P. J. B. HART.
1982. Fisheries ecology. Avi Publ. Co. Inc., Westport, Conn., 414 p.

POWLES, H., AND C. A. BARANS.
1980. Groundfish monitoring in sponge-coral areas off the southeastern United States. Mar. Fish. Rev. 42(5):21-35.

RALSTON, S.
1980. An analysis of the Hawaiian offshore handline fishery: A progress report. *In* R. W. Grigg and R. T. Pfund (editors), Proceedings of the Symposium on Status of Resource Investigations in the Northwestern Hawaiian Islands, April 24-25, 1980, University of Hawaii, Honolulu, Hawaii, p. 216-225. Sea Grant Misc. Rep. UNIHI-SEAGRANT-MR-80-04.
1984. Biological constraints on production and related management issues in the Hawaiian deepsea handline fishery. *In* R. W. Grigg and K. Y. Tanoue (editors), Proceedings of the Symposium on Resource Investigations in the Northwestern Hawaiian Islands, May 25-27, 1983, University of Hawaii, Honolulu, Hawaii, p. 248-264. Sea Grant Misc. Rep. UNIHI-SEAGRANT-MR-84-01.

RALSTON, S., AND G. T. MIYAMOTO.
1983. Analyzing the width of daily otolith increments to age the Hawaiian snapper, *Pristipomoides filamentosus*. Fish. Bull., U.S. 81:523-535.

RALSTON, S., AND J. J. POLOVINA.
1982. A multispecies analysis of the commercial deep-sea handline fishery in Hawaii. Fish. Bull., U.S. 80:435-448.

RANDALL, J. E., P. S. LOBEL, AND E. H. CHAVE.
In press. Annotated checklist of the fishes of Johnston Island. Pac. Sci.

RICKER, W. E.
1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull. 191, 382 p.

ROTHSCHILD, B. J.
1977. Fishing effort. *In* J. A. Gulland (editor), Fish population dynamics, p. 96-115. John Wiley and Sons, N.Y.

SALE, P. F., AND W. A DOUGLAS.
1981. Precision and accuracy of visual census technique for fish assemblages on coral patch reefs. Environ. Biol. Fishes 6:333-339.

SHIPP, R. L., AND T. S. HOPKINS.
1978. Physical and biological observations of the northern rim of the De Soto Canyon made from a research submersible. Northeast Gulf Sci. 2(2):113-121.

STRASBURG, D. W., E. C. JONES, AND R. T. B. IVERSEN.
1968. Use of a small submarine for biological and oceanographic research. J. Cons. Cons. Perm. Int. Explor. Mer 31:410-426.

TALBOT, F. H.
1960. Notes on the biology of the Lutjanidae (Pisces) of the East African coast, with special reference to *L. bohar* (Forskal). Ann. S. Afr. Mus. 45:549-573.

THORNE, R. E.
1983. Hydroacoustics. *In* L. A. Nielsen, D. L. Johnson, and S. S. Lampton (editors), Fisheries techniques, p. 239-259. Am. Fish. Soc., Bethesda, MD.

UZMANN, J. R., R. A. COOPER, R. B. THEROUX, AND R. L. WIGLEY.
1977. Synoptic comparison of three sampling techniques for estimating abundance and distribution of selected megafauna: Submersible vs camera sled vs otter trawl. Mar. Fish. Rev. 39(12):11-19.

PATCHINESS AND NUTRITIONAL CONDITION OF ZOOPLANKTON IN THE CALIFORNIA CURRENT

STEWART W. WILLASON, JOHN FAVUZZI, AND JAMES L. COX[1]

ABSTRACT

Zooplankton and water samples were collected from 81 stations off the California coast in April 1981 during CalCOFI cruise 8104 aboard the RV *David Starr Jordan*. Abundance, weight (wet and dry), digestive enzyme activity (laminarinase), and biochemical composition of three zooplankton species were determined. The indices measured provided estimates of zooplankton nutritional history on time scales of 1 day to 3 weeks.

Upwelling was taking place along the California coast, from Point Conception to San Francisco during the study period. The resulting low surface temperatures were most evident south of San Francisco and just north of Point Conception. Just south of these areas patches of high phytoplankton standing crop (up to 14.7 mg chlorophyll a/m^3) were found. The two herbivorous species, *Euphausia pacifica* and *Calanus pacificus*, showed highest laminarinase activity in areas with the highest density of phytoplankton: enzyne activity was particularly high in the waters off Point Conception. Zooplankters in the southern and offshore regions of the sampling grid showed very low digestive enzyme activity. The larger size (weight) and higher lipid content of *C. pacificus* near Point Conception and south of San Francisco in comparison to animals in other parts of the California Current suggest that animals in these areas experience prolonged periods of better nutrition. *Nematoscelis difficilis*, which is not a herbivore, did not show these patterns. This study illustrates the importance of upwelling regions, such as Point Conception, and shows the large spatial variability of trophic interactions within the California Current System.

The nearshore, pelagic marine environment is extremely variable and heterogeneous. Spatial heterogeneity of physical conditions elicit behavioral or physiological responses from marine organisms which contribute to biological patchiness (Haurey et al. 1978; Steele 1978). Patchiness of pelagic marine organisms occurs on all temporal and spatial scales (Haury et al. 1978); one of the most important of these is the mesoscale (a few kilometers to 100's of kilometers, and a few weeks to months). Mesoscale processes, such as coastal upwelling, play a major role in structuring the physical and biological environment at all scales (Haury 1982). Although upwelling regions are very productive (e.g., Ryther 1969), trophic interactions within these important areas are poorly understood.

Along the California coast episodic upwelling takes place during the spring and summer months (Reid et al. 1958; Bernstein et al. 1977; Owen 1980; Lasker et al. 1981; Parrish et al. 1981). Upwelling results in mesoscale phytoplankton patchiness along the coast and in the southward flowing California Current (Owen 1974; Cox et al. 1982; Smith and Baker 1982; Pelaez and Guan 1982). It is thought that phytoplankton patchiness in this area influences the survival and physiological condition of larval fish populations (Lasker 1975; Lasker and Smith 1977; Lasker and Zweifel 1978; O'Connell 1980). In addition, nutrition of herbivorous zooplankton (estimated by digestive enzyme activity) is influenced by phytoplankton patchiness (Cox et al. 1982; Cox et al. 1983; Willason and Cox in press).

This study investigates the impact that mesoscale and larger scale phytoplankton patchiness have on zooplankton populations within the California Current along the central and southern California coast. Results of measurements of temperature, phytoplankton biomass, zooplankton abundance, and zooplankton nutrition are presented. Nutritional status was evaluated using intrinsic properties which reflect previous feeding conditions. Short-term feeding history was estimated from measurements of the activity of the digestive enzyme, laminarinase. Although digestive enzyme levels of zooplankton do not always provide a good measure of instantaneous digestive or feeding rates (Hassett and Landry 1983; Head et al. 1984; Willason and Cox in press), the level of activity in field captured animals does give an indication of relative feeding history on the order of 1 to 5 d (Cox 1981; Cox and Willason 1981; Cox et al. 1983; Willason 1983). Longer term nutritional condition was assessed from biochemical composition and animal size (wet and dry weight) measurements.

[1]Marine Science Institute, University of California, Santa Barbara, CA 93106.

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Lipid content, size, and water content of a zooplankton species reflect feeding history on the order of 1 to 3 wk (Omori 1970; Lee et al. 1970, 1971; Bamstedt 1975; Childress 1977; Boyd et al. 1978; Vidal 1980; Hakanson 1984). Spatial patterns derived from these data are used to estimate relative differences in feeding and nutritional condition of zooplankton from different areas within the California Current. An understanding of the interrelationships of these variables in different areas may provide insights into mechanisms which generate and maintain physical and biological mesoscale features.

METHODS

Species Studied

Two euphausiid species, *Euphausia pacifica* Hansen and *Nematoscelis difficilis* Hansen, and the copepod, *Calanus pacificus* Brodsky, were chosen for the present study because 1) all are common in the California Current region (Fleminger 1964; Brinton 1967b), 2) all have been used in previous digestive enzyme studies (Cox 1981; Cox and Willason 1981; Hassett and Landry 1982, 1983; Cox et al. 1983; Willason 1983; Willason and Cox in press), and 3) a large base of information exists on the sizes, feeding rates, and energetics of these zooplankters (Brinton 1967a; Mullin and Brooks 1976; Vidal 1980; Ross 1982; Cox et al. 1983; Torres and Childress 1983; Willason 1983; Hakanson 1984; Willason and Cox in press). *Euphausia pacifica*, the most abundant euphausiid in the California Current (Brinton 1967b; Brinton and Wyllie 1976; Youngbluth 1976), and *C. pacificus*, the most abundant copepod along the California coast (Fleminger 1964; Star and Mullin 1981), are considered primarily herbivorous (Mullin and Brooks 1976; Ross 1982; Willason and Cox in press). By contrast, *N. difficilis* does not appear to be a herbivore (Nemoto 1967; Mauchline and Fisher 1969; Willason and Cox in press).

Sample Collection

The sampling program was conducted off the California coast from 7 to 27 April 1981 in conjunction with the California Cooperative Fisheries Investigation (CalCOFI) survey. Zooplankton and water samples were collected from 81 stations during CalCOFI cruise 8104 aboard RV *David Starr Jordon*. Figure 1 shows the stations sampled and the sampling sequence during the cruise. The grid covered an area of about 270,000 km^2; nearshore stations were sometimes within 1 km of the coast and offshore stations were located up to 300 km from the coast.

Although the mean flow of the California Current is south through the sampling grid at this time of the year (Lynn et al. 1982), smaller regions within the grid are often subjected to different hydrographic influences. For example, the waters of the offshore regions intergrade with the waters of the Central Pacific Gyre (Bernstein et al. 1977); the nearshore region south of Point Conception (the Southern California Bight) is characterized by a semipermanent, counterclockwise eddy and is hydrographically distinct from the other areas of the grid (Owen 1980); and the nearshore area adjacent to and north of Point Conception is characterized by periods of intense coastal upwelling during the spring and summer months (Parrish et al. 1981). To compare the biological and nutritional properties of zooplankton in the different hydrographic regions, the sampling grid was divided into four sections: southern nearshore (I), northern nearshore (II), southern offshore (III), and northern offshore (IV) (Fig. 1).

Surface chlorophyll a concentration (depth of 2 m) was used as an indicator of phytoplankton standing crop. Previous studies have shown that there are positive correlations between surface chlorophyll a, integrated chlorophyll a, and primary production in the waters of the California Current (Lorenzen 1970; Hayward and Venrick 1982). Measurements of surface chlorophyll a, therefore, give a relative approximation of phytoplankton biomass within the sampling grid.

Two replicate water samples (0.25 to 2.0 L) for chlorophyll a analysis were taken at each of the 81 stations from a depth of about 2 m using the ship's seawater pumping system. Each sample was filtered through a 4.5 cm Whatmann GF/C filter; two drops of a seawater-saturated $MgCO_3$ solution were added during filtrations. The filters were folded in half and stored frozen in aluminum foil at −20°C. An additional 15 water samples were taken for chlorophyll a analysis along the cruise track adjacent to and immediately south of the Point Conception region while the ship was under way. Measurements of surface water temperature (±0.1°C) were also taken at each station using a glass mercury thermometer.

Paired bongo nets (designated net 1 and net 2) with mouth openings of 0.396m^2 and mesh openings of 505 μm were used for the collection of zooplankton samples. A General Oceanics[2] flowmeter was mount-

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

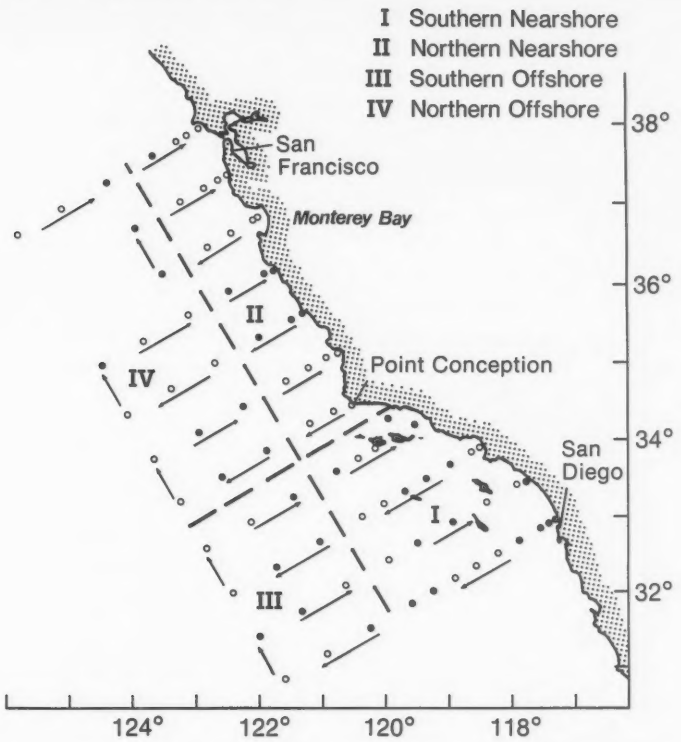

FIGURE 1.—Sampling grid. Open circles are day stations and closed circles are night stations. Arrows show the sampling sequence. The first station, adjacent to San Diego, was occupied on 7 April 1981. The last station, just north of San Francisco, was occupied on 27 April 1981.

ed inside the mouth of each net to measure the volume of water filtered. An oblique net tow was made to a depth of about 210 m at each station (bottom depth permitting); each net filtered about 400 m^3 of water. Ship speed during the net tows was 1.5 to 2.0 kn. Thirty-six stations were occupied at night (after sunset and before sunrise) and 45 were occupied during the day.

The euphausiids, *Euphausia pacifica* and *Nematoscelis difficilis*, and the copepod, *Calanus pacificus*, were separated from the catch of net 1 immediately after collection. Adult euphausiids were sorted for males and females and copepods sorted for females and stage V copepodites. Specimens of *E. pacifica* and *N. difficilis* were considered adults if they were larger than 11 mm and 15 mm, respectively (Brinton and Townsend 1981). Fifty undamaged animals of each species and sex (or stage) were saved from each net tow if adequate numbers were captured. For *C. pacificus*, which were very abundant, 50 females and stage V's were saved from 72 and 75 of the 81 stations, respectively. Two replicate groups of 50 females of *C. pacificus* were taken from 7 stations and two replicate groups of 50 stage V copepodites from 9 stations. After sorting, animals from each net tow were wrapped in parafilm in groups (5 to 50 animals of each sex or stage) and frozen at −20°C for biochemical analyses in the laboratory. Catches from net 1 that could not be sorted on the ship (10 of the 81 stations sampled) were frozen whole at −20°C and sorted in the laboratory after the cruise. The entire catch of net 2 was preserved in Formalin immediately after collection.

The abundances (numbers per 1,000 m^3) of adult euphausiids at each station were estimated by counting all adults captured in net 1 and dividing by the volume of water filtered. Copepod abundances (numbers per 1 m^3) were estimated by counting all

females and stage V copepodites in triplicate aliquots taken from the preserved catches of net 2.

Sample Analyses

All frozen samples were analyzed in the laboratory within 6 wk of the time of collection. Plant pigments were extracted from the filters in 90% acetone in darkness at 4°C for 48 h. Chlorophyll a concentration was determined by the method of Strickland and Parsons (1972) using a model 10-005 Turner Designs fluorometer. The two chlorophyll a measurements from each station were averaged.

Groups of frozen animals (separate species and sexes) were thawed in the laboratory, blotted lightly to remove excess water, and weighed (±0.01 mg). Animals were then freeze-dried for 24 h at −50°C and reweighed. Groups were then immediately ground in cold (4°C) succinic acid buffer (pH 5.0) using a Polytron grinder (for euphausiids) or a hand glass tissue grinder (for copepods). Homogenates were analyzed for total proteins by the Lowry method using Sigma protein standard (Merchant et al. 1964). Laminarinase activity (LA) of the homogenates was determined by the methods described by Cox (1981) and Willason (1983). LA was expressed as a function of the animal's wet weight: μg glucose produced per gram wet weight per minute of incubation. Copepod homogenates were also analyzed for total lipids using stearic acid as the standard (Bligh and Dyer 1959; Marsh and Weinstein 1966).

Data Analysis

Willason and Cox (in press) found that *E. pacifica* exhibits a diel rhythm in enzyme activity associated with feeding activity at night. Thus, to compare LA of *E. pacifica* collected at different times of the day from different localities, enzyme levels had to be standardized with respect to the time of capture. Calibration factors, which convert the LA of *E. pacifica* collected at different times to a standardized maximum value (between 0200 and 0800 h), were derived from the results of the 24-h time-series collections in Willason and Cox (in press). These factors are based on the average relative increases and decreases of enzyme activity over a 24-h period (Table 1). LA of *N. difficilis* and *C. pacificus* do not show diel changes (Cox et al. 1983; Willason and Cox in press) and, therefore, were not standardized.

The data set for each station consists of surface temperature, surface chlorophyll a, zooplankton abundance, LA, individual wet and dry weights, protein content, and lipid content (copepods only). To permit parametric statistical comparisons between the various biological and physical properties and between regions, chlorophyll a, zooplankton abundance, and zooplankton LA were normalized by log transformation. The log transformed values were used for all parametric statistical tests. Zooplankton wet weight, dry weight, protein content, and lipid content were found to be normally distributed by probit analysis and were not log transformed. Nontransformed values from all data sets were used to construct contour maps. The contour maps are intended to show general trends and patchiness within the sampling grid.

TABLE 1.—Correction factors for standardizing laminarinase activity (LA) of *Euphausia pacifica*. These factors account for diel changes in LA and are based on the time of capture. They were derived from the 24-h time-series collections of Willason and Cox[1]. LA was standardized to the 0200-0800 time period. LA of euphausiids captured during other time periods was multiplied by the corresponding factor.

	Correction factor	
Time period	Females	Males
2000-0200	1.042	1.132
0200-0800	1.000	1.000
0800-1400	1.253	1.281
1400-2000	1.486	1.453

[1]Willason, S. W., and J. L. Cox. In press. Diel feeding, laminarinase activity and phytoplankton consumption by euphausiids. Biol. Oceanogr.

RESULTS

Surface Water Temperature and Surface Chlorophyll a

Surface water temperatures along the California coast during April 1981 ranged from 9.6° to 16.0°C. The coldest water was located in the northern nearshore region and the warmest was found in the southern offshore region (Table 2, Fig. 2). Two small areas showed very low surface water temperatures: close to the shore along the central coast of California and just off San Francisco Bay (Fig. 2). A cold water plume extended from Point Conception south into the Southern California Bight.

Chlorophyll a concentrations showed greater than 100-fold variation between stations and were inversely correlated with surface water temperatures (r = 0.83, $P < 0.001$). Lowest values, 0.09 to 0.16 mg chlorophyll a/m^3, were found in the southern offshore region. Highest concentrations occurred in the northern nearshore region (Table 2, Fig. 3). Within

TABLE 2.—Mean surface water temperature and mean surface chlorophyll a. Chlorophyll a expressed as mg/m^3. The numbers in parentheses are one standard deviation.

	Southern Nearshore (I)	Southern Offshore (III)	Northern Nearshore (II)	Northern Offshore (IV)
Temperature (°C)	14.85 (0.72)	15.03 (0.49)	11.56 (0.82)*	13.68 (0.78)
Chlorophyll a	0.659 (0.88)	0.141 (0.04)	5.110 (4.42)	0.485 (0.29)
Log Chlorophyll a	−0.378 (0.38)	−0.883 (0.12)	0.555 (0.39)*	−0.404 (0.31)
No. of stations	27	12	25	17

* indicates value(s) significantly different from those of other regions ($P < 0.05$, t-test).

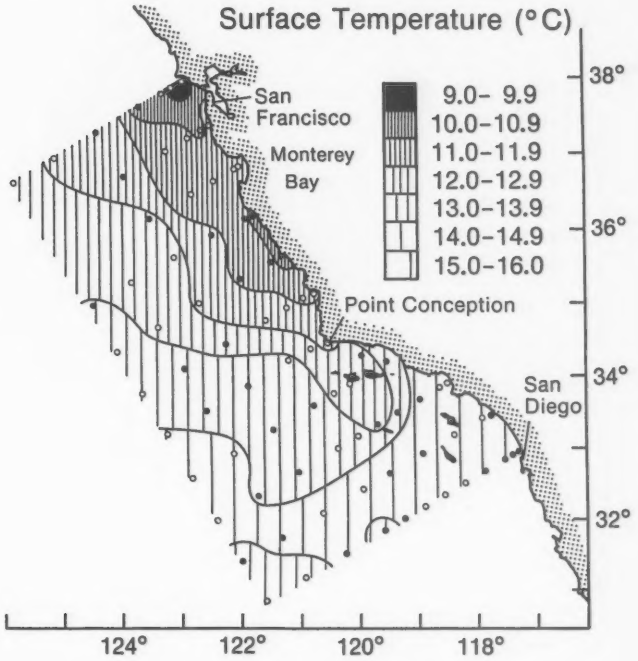

FIGURE 2.—Surface water temperatures (°C) along the California coast.

this region two areas of very high chlorophyll a (up to 14.7 mg/m^3) were found: near Point Conception and just south of San Francisco Bay. These areas were located just south of the areas of coldest surface waters.

Euphausiid Distribution and Abundance

Euphausia pacifica adults were captured at 43 of the 81 stations sampled and *Nematoscelis difficilis* adults were captured at 38 stations. As there was no significant difference between numbers of males and females captured of either species ($P > 0.3$, Wilcoxon test), the abundances shown in Figures 4 and 5 represent the sum of both sexes. Both the number of specimens of *N. difficilis* captured at each station ($P < 0.01$, t-test) and the proportion of stations where individuals were caught ($P < 0.01$, χ^2 test) were greater at night. For *E. pacifica*, there were no significant day-night differences in the numbers of animals captured ($P > 0.2$, t-test), however, like *N. difficilis*, the proportion of stations where individuals were captured was greater at night ($P < 0.05$, χ^2 test). The day-night differences may represent net avoidance by euphausiids or undersampling during the day because of vertical migration. Thus, the data presented in Figures 4 and 5 represent general trends and are intended to show relative differences between areas. Because euphausiids were captured at only about one half of the stations, statistical comparisons were made only between the north and south (i.e., nearshore and

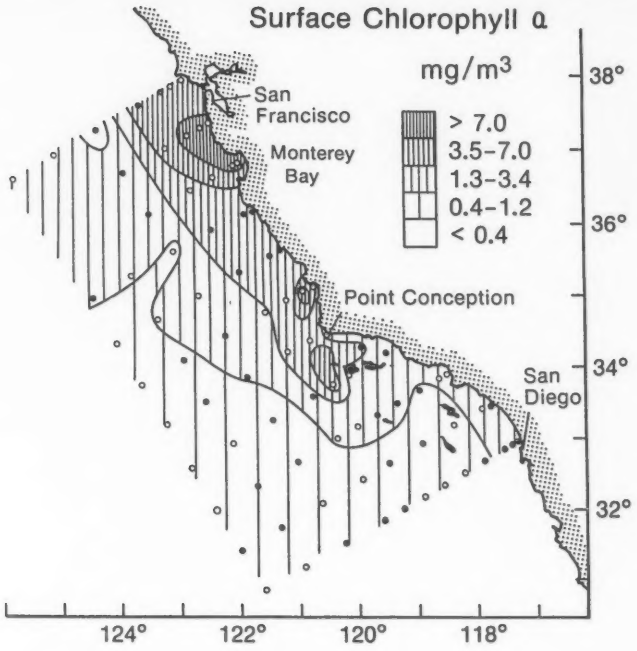

FIGURE 3.—Surface chlorophyll a. Expressed as mg chlorophyll a per m^3.

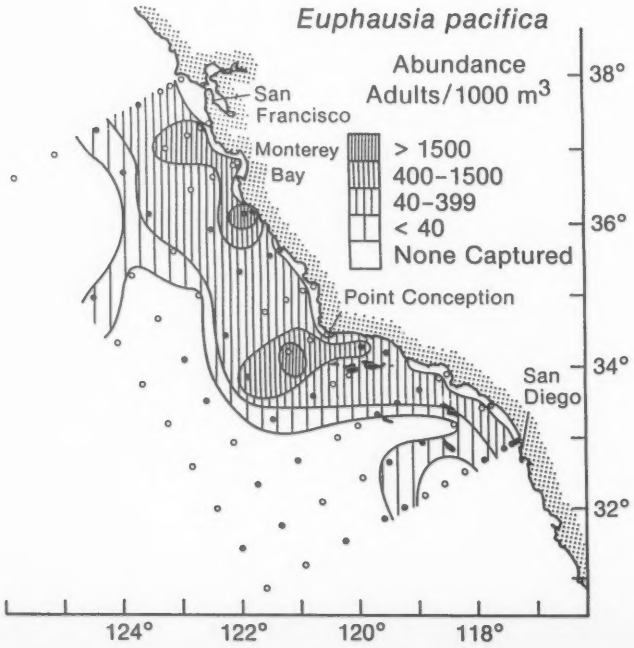

FIGURE 4.—*Euphausia pacifica* abundance. Expressed as number of adults per 1,000 m^3.

offshore regions for the north and south were combined).

Specimens of *E. pacifica* were captured in significantly greater numbers north of Point Conception (Table 3) and were rare or absent at most offshore stations (regions III and IV). This species was especially abundant off Point Conception and just south of Monterey Bay along the central coast (Fig. 4). These two areas were located close to the areas of highest chlorophyll a concentration. The abundance of *E. pacifica* was significantly correlated with chlorophyll a over the entire grid (Table 4).

The distribution of *N. difficilis* (Fig. 5) was quite different from that of *E. pacifica*. This species was captured at only 30% of the stations where *E. pacifica* was found and was distributed farther off-

TABLE 3.—Mean abundance and laminarinase activity (LA) of *Euphausia pacifica* and *Nematoscelis difficilis* in the north and south regions. Numbers in parentheses are one standard deviation. Log values were used for statistical comparisons.

	South Regions (I & III)		North (Regions (II & IV)	
	Males	Females	Males	Females
Euphausia pacifica				
Abundance (No./1,000 m^3)	96.07 (100.4)	96.41 (102.5)	200.6 (234.4)	270.2 (337.3)
Log abundance	1.604 (0.623)*	1.647 (0.666)*	2.035 (0.551)	2.119 (0.579)
LA	122.5 (47.8)	165.1 (59.9)	109.7 (68.9)	153.2 (111.9)
Log LA	2.058 (0.167)	2.186 (0.183)	1.965 (0.263)	2.099 (0.269)
No. of stations	16	15	27	27
Nematoscelis difficilis				
Abundance (No./1,000 m^3)	13.71 (12.78)	18.06 (16.07)	55.11 (70.31)	75.17 (83.84)
Log abundance	1.001 (0.327)*	1.061 (0.461)*	1.530 (0.441)	1.657 (0.453)
LA	167.3 (87.5)	208.6 (102.9)	104.4 (41.9)	130.4 (55.1)
Log LA	2.172 (0.237)*	2.270 (0.207)*	1.992 (0.174)	2.041 (0.191)
No. of stations	16	18	20	19

* indicates value(s) significantly different between north and south ($P < 0.05$, *t*-test).

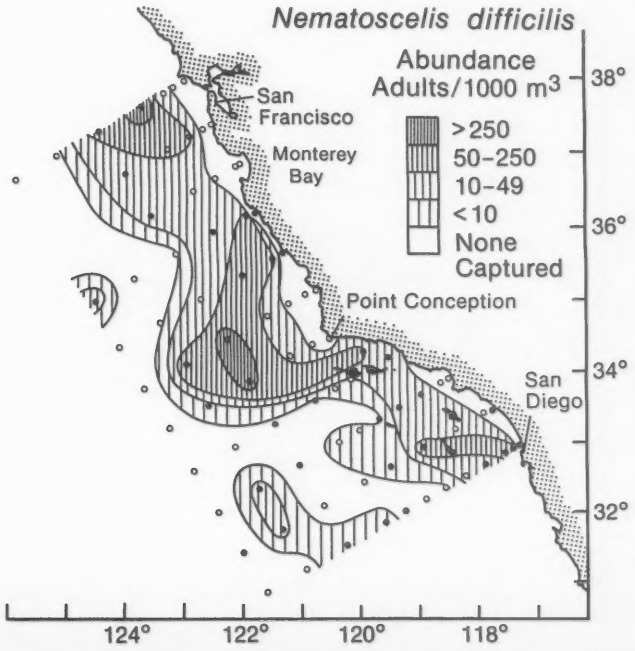

FIGURE 5.—*Nematoscelis difficilis* abundance. Expressed as number of adults per 1,000 m^3.

shore. As with *E. pacifica*, both sexes of *N. difficilis* were found in significantly greater numbers in the north (Table 3). The abundance of *N. difficilis* was not correlated with surface chlorophyll a (Table 4).

Euphausiid Laminarinase Activity

Similar to the results of Willason (1983) and Willason and Cox (in press), males of both euphausiid species showed significantly less LA than females ($P < 0.01$, both cases, Wilcoxon test). Males in this study had about 70% (*Euphausia pacifica*) or 80% (*Nematoscelis difficilis*) of the LA of females (Table 3). To simplify the presentation of the data on the contour maps, LA values of males and females at each station were averaged.

The values of LA for *Euphausia pacifica* within the sampling grid ranged from 50 to 430. Euphausiids with the lowest LA values were found in offshore areas and in the nearshore area along the central coast. *Euphausia pacifica* with the highest levels of LA were found just south of San Francisco Bay and adjacent to the south of Point Conception (Fig. 6). These areas overlapped with and extended just south of the regions of highest surface chlorophyll a. There was a positive correlation between LA of *E. pacifica* and chlorophyll a over the entire grid (Table 4).

TABLE 4.—Correlations between chlorophyll a, zooplankton abundance, and laminarinase activity (LA) for *Euphausia pacifica*, *Nematocelis difficilis*, and *Calanus pacificus*. For euphausiids, abundance and LA values used in the analyses are the averages of males and females. Numbers in parentheses refer to the number of samples used in regression analyses.

	Correlation coefficients			
Correlation	*E. pacifica* (43)	*N. difficilis* (38)	*C. pacificus* ♀ (81)	*C. pacificus* V (81)
Chlorophyll a vs. abundance	0.61	[1]0.27	0.24	0.31
Chlorophyll a vs. LA	0.57	[1]0.03	0.53	0.62
LA vs. abundance	0.40	[1]0.14	0.38	0.48

[1]Correlation coefficients which were not significant at the 95% level.

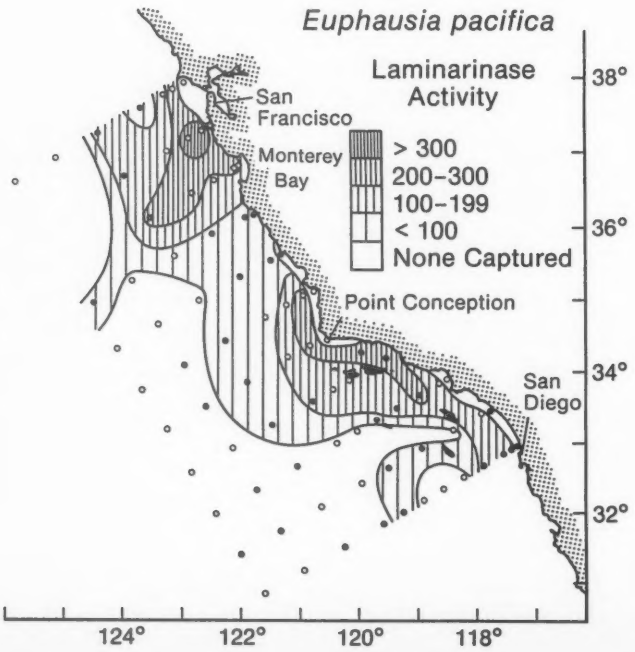

FIGURE 6.—*Euphausia pacifica* laminarinase activity (LA). Expressed as μg glucose per gram wet weight per minute.

The values of LA for *Nematoscelis difficilis* were in the same range as those of *Euphausia pacifica* (50 to 400), but showed a different distributional pattern (Fig. 7). Regions of highest activity were located in three small areas: adjacent to San Diego, in the Santa Barbara Channel (just south of Point Conception), and in an area about 150 km off Monterey Bay. Both males and females of *N. difficilis* had significantly higher levels of LA in the southern portion of the grid (Table 3). LA of *N. difficilis* was not correlated with chlorophyll a (Table 4). *Nematoscelis difficilis* with high LA were often found in areas with very low phytoplankton biomass and vice versa.

Euphausiid Size and Chemical Composition

Mean wet and dry weights, water content, and protein content (expressed as percent dry weight and percent wet weight) of *Euphausia pacifica* and *Nematoscelis difficilis* are presented in Table 5. Female *E. pacifica* and both sexes of *N. difficilis* had significantly higher wet and dry weights in the north. The water content of both euphausiid species ranged from 76.5 to 81.7% and was very similar between species, sexes, and regions (Table 5). Protein content was also very similar between species, sexes, and regions. The protein values reported here (51 to 56% of dry weight) are within the range of previously reported values (Childress and Nygaard 1974).

Copepod Distribution and Abundance

Female and stage V copepodites of *Calanus pacificus* were captured at all 81 stations sampled. There were no significant differences between day and night catches for either *C. pacificus* ($P < 0.01$, *t*-test). For comparisons between regions, mean abundances were calculated using both the log transformed and nontransformed values (Table 6). The log transformed values were used for statistical comparisons. The overall abundances of females and stage V copepodites were similar to one another in all regions ($P > 0.1$, *t*-test, all cases). Both *C. pacificus* stages were significantly more abundant in the two nearshore regions (I and II) than in the two offshore regions (III and IV) (Table 6). Figures 8 and 9 show that the distributions of females and stage V *C. pacificus* were patchy within regions. Copepods were particularly abundant in the area close to and just south of Point Conception. An extremely dense aggrega-

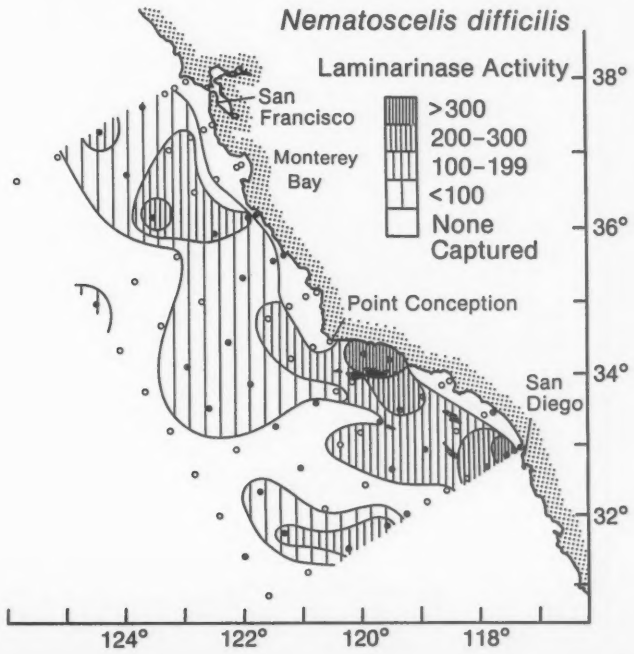

FIGURE 7.—*Nematoscelis difficilis* laminarinase activity (LA). Expressed as μg glucose per gram wet weight per minute.

TABLE 5.—Mean individual wet weight, dry weight, % water, and protein content of *Euphausia pacifica* and *Nematoscelis difficilis* from the north and south. Numbers in parentheses are one standard deviation.

	South (Regions I & III)		North (Regions II & IV)	
	Males	Females	Males	Females
Euphausia pacifica				
Wet weight (mg)	31.01 (11.55)	32.57 (10.81)*	37.73 (11.24)	42.38 (12.11)*
Dry weight (mg)	6.48 (2.38)	6.75 (2.53)*	7.91 (2.57)	8.98 (2.41)*
% water	79.10	79.28	79.04	78.81
Protein (% dry wt)	54.57	56.16	52.62	52.26
Protein (% wet wt)	11.40	11.62	11.05	11.02
No. of stations	16	15	27	27
Nematoscelis difficilis				
Wet weight (mg)	27.63 (7.07)*	34.73 (11.28)*	35.23 (7.26)*	43.59 (8.72)*
Dry weight (mg)	5.96 (2.21)	7.22 (2.49)*	7.43 (2.22)	9.19 (2.78)*
% water	78.43	79.22	78.82	78.94
Protein (% dry wt)	56.59	51.23	52.92	54.96
Protein (% wet wt)	12.22	10.65	11.17	11.58
No. of stations	16	18	20	19

* indicates value(s) significantly different between north and south ($P < 0.05$, *t*-test).

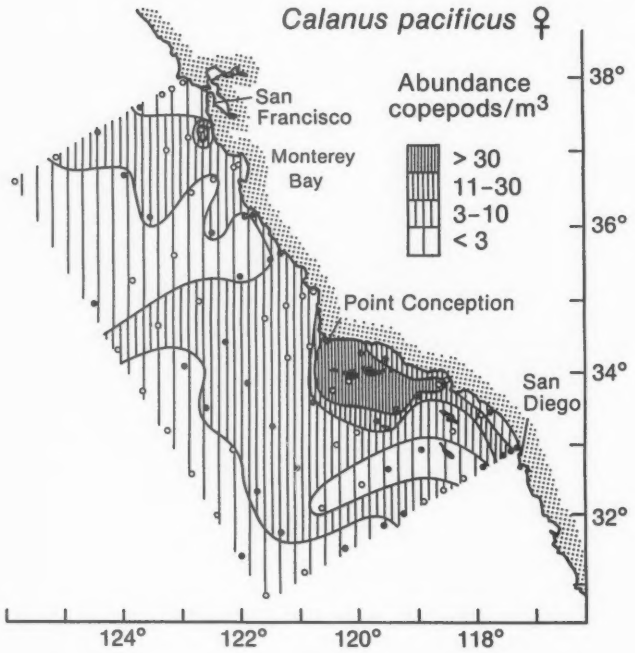

FIGURE 8.—*Calanus pacificus* females, abundance. Expressed as number of copepods per m^3.

tion of stage V *C. pacificus* (474 copepods/m^3) was found at the station adjacent to Point Conception. The areas where *C. pacificus* showed the highest abundances were located near regions of high chlorophyll a concentration. However, the abundances of both *C. pacificus* stages were poorly correlated (although significant at the 95% level) with chlorophyll a over the entire grid (Table 4).

Copepod Laminarinase Activity

LA of female and stage V copepodites was much higher than the levels of both euphausiid species when expressed on a per weight basis. Like the euphausiid results, there was large variability in the LA of *C. pacificus* among stations. For example, LA of stage V copepodites ranged from <150 at offshore

TABLE 6.—*Calanus pacificus*. Mean abundance and laminarinase activity (LA) of stage V copepodites and females from each region. Numbers in parentheses are one standard deviation. Log values were used for statistical comparisons.

	Southern Nearshore (I)	Southern Offshore (III)	Northern Nearshore (II)	Northern Offshore (IV)
Stage V copepodites				
Abundance (No./m^3)	22.89 (32.11)	1.70 (0.86)	26.07 (93.90)	1.82 (1.44)
Log abundance	0.924 (0.681)*	0.175 (0.233)	0.571 (0.733)*	0.139 (0.299)
LA	825.4 (455)	538.6 (254)	1,527.5 (792.1)	933.2 (659.4)
Log LA	2.845 (0.272)	2.688 (0.201)	3.129 (0.231)*	2.891 (0.258)
Females				
Abundance (No./m^3)	14.21 (14.72)	2.54 (2.21)	6.67 (10.79)	3.05 (2.03)
Log abundance	0.807 (0.692)*	0.253 (0.411)	0.621 (0.400)*	0.343 (0.351)
LA	927.6 (466.2)	635.2 (413.5)	1,272.9 (610.3)	1,041.5 (547.5)
Log LA	2.913 (0.281)	2.734 (0.222)	3.072 (0.204)*	2.856 (0.261)
No. of stations	27	12	25	17

* indicates value(s) significantly greater than those of other regions ($P < 0.05$, *t*-test).

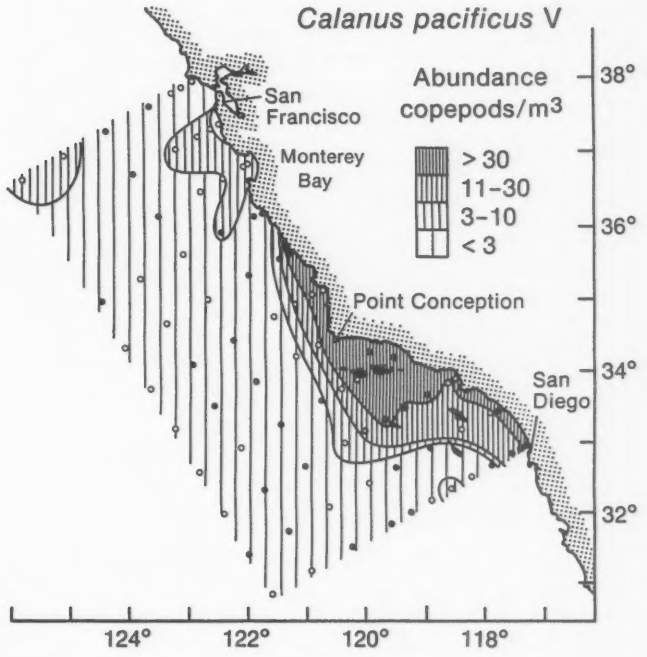

FIGURE 9.—*Calanus pacificus* Stage V copepodites, abundance. Expressed as number of copepods per m^3.

stations to 3,855 at the station adjacent to Point Conception. LA of replicate groups of 50 copepods from the same station were very similar indicating that the variability was due to differences between stations ($P < 0.05$, ANOVA).

Calanus pacificus LA also showed large differences among the four hydrographic regions. Both females and stage V copepodites from the northern nearshore region (II) had significantly higher levels of LA than copepods from the other regions (Table 6). Copepods in the southern offshore region had the lowest levels. The contour maps of *C. pacificus* LA show patches of copepods with high LA located adjacent to and just south of Point Conception and off Monterey Bay (Figs. 10, 11). These areas were located near the regions of highest *E. pacifica* LA (Fig. 6) and close to the regions of highest chlorophyll a (Fig. 3). There were significant positive cor-

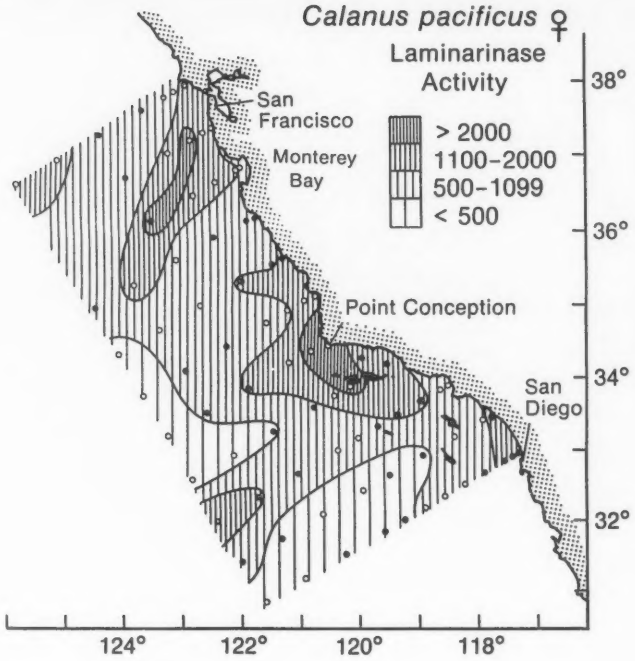

FIGURE 10.—*Calanus pacificus* females, laminarinase activity (LA). Expressed as μg glucose per gram wet weight per minute.

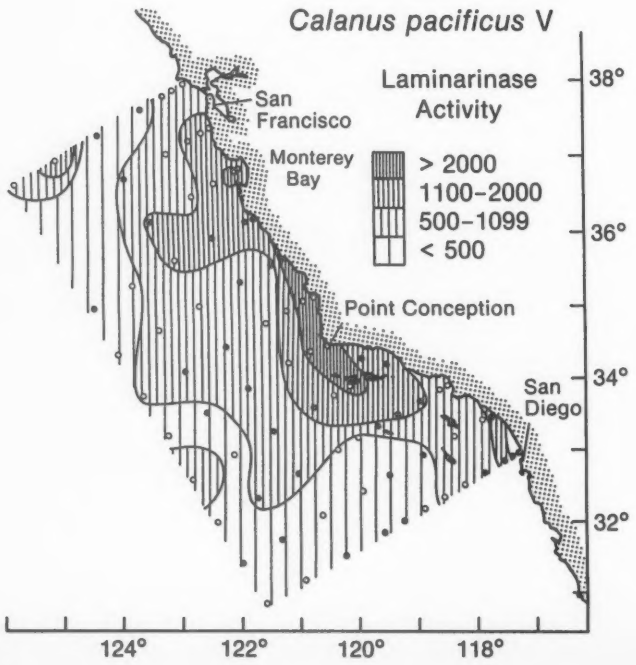

FIGURE 11.—*Calanus pacificus* Stage V copepodites, laminarinase activity (LA) Expressed as μg glucose per gram wet weight per minute.

relations between the LA of both *C. pacificus* stages and the concentration of chlorophyll a (Table 4).

Copepod Wet and Dry Weights

The largest female and stage V *C. pacificus* in terms of weight were located in the northern nearshore region and the smallest copepods were found in the southern regions (Table 7). The average water content of both *C. pacificus* stages from the four regions was inversely related to the average dry weights. Specimens of *C. pacificus* with the lowest water content were found in the northern nearshore region and those with highest water content were located in the southern offshore region (Table 7).

Figures 12 and 13 show the distribution of wet weights of *C. pacificus* females and stage V copepodites, respectively. Since wet and dry weights were highly correlated ($r = 0.81$ and 0.83, $P < 0.001$) only wet weights are shown. Both figures show a band of large copepods in the nearshore region along the central coast. The figures also show the variation in size of each stage between areas. Copepods (both stages) in the "heavy band" along the central coast were almost twice the weight of copepods at some of the offshore and southern stations.

Copepod Protein and Lipid Content

Total protein content (μg per copepod) of both *C. pacificus* stages was highest in the northern nearshore region and lowest in the two southern regions (Table 7). This appears to reflect differences in copepod size between regions as there were highly significant correlations between the protein content and the wet weight for both female ($r = 0.82$, $P < 0.001$) and stage V *C. pacificus* ($r = 0.69$, $P < 0.001$). Protein content was not mapped since the patterns were very similar to those of wet weight.

Protein content of *C. pacificus*, expressed as percent of wet weight, was quite similar between regions: 8.9 to 10.5% for stage V copepodites and 9.3 and 10.8% for females (Table 7). However, both stages from the southern offshore region did show slightly higher protein content when expressed as percent dry weight. This probably reflects the high water content of copepods from the southern offshore region.

The distributions of lipid content of female and stage V *C. pacificus* were very patchy and showed greater than fourfold variation between areas (Figs. 14, 15). Copepods with highest lipid values were found in the area surrounding Point Conception and off San Francisco Bay. Although copepod size (wet weight) probably influenced the total lipid content of *C. pacificus* to some extent, the variability of lipid content cannot be attributed solely to weight. Lipid content, unlike protein content, was poorly correlated with wet weight ($r = 0.26$ for females and $r = 0.38$ for stage V copepodites).

TABLE 7.—*Calanus pacificus*. Mean wet weight, dry weight, percent water, protein content, and lipid content for stage V copepodites and females from each region. Numbers in parentheses are one standard deviation.

	Southern Nearshore (I)	Southern Offshore (III)	Northern Nearshore (II)	Northern Offshore (IV)
Stage V copepodites				
Wet weight (μg)	471 (81)	447 (83)	555 (92)*	465 (95)
Dry weight (μg)	98 (21)	88 (23)	125 (26)*	98 (25)
% water	79.20	80.31	77.54	78.89
Protein (μg/copepod)	41.88 (12.24)	44.82 (9.31)	52.15 (11.26)	48.58 (8.02)
Protein (% dry wt)	44.12	49.25	42.75	48.10
Protein (% wet wt)	8.89	10.03	9.40	10.45
Lipid (μg/copepod)	19.74 (7.82)	13.94 (4.96)	29.33 (7.72)*	15.74 (5.71)
Lipid (% dry wt)	20.78	15.32	24.04	15.58
Lipid (% wet wt)	4.19	3.12	5.28	3.38
Females				
Wet weight (μg)	1,023 (170)	1,083 (160)	1,278 (180)*	1,125 (190)
Dry weight (μg)	191 (47)	185 (38)	263 (40)*	225 (29)
% water	81.34	82.83	79.40	80.20
Protein (μg/copepod)	94.92 (22.71)	100.84 (24.84)	137.81 (26.40)*	115.62 (23.33)
Protein (% dry wt)	49.70	54.51	52.74	51.38
Protein (% wet wt)	9.28	9.31	10.78	10.28
Lipid (μg/copepod)	26.71 (13.31)	21.96 (9.00)	35.27 (11.47)	30.19 (10.21)
Lipid (% dry wt)	13.81	11.69	13.41	13.47
Lipid (% wet wt)	2.61	2.03	2.76	2.68
No. of stations	27	12	25	17

* indicates value(s) significantly greater than those of other regions ($P < 0.05$, *t*-test).

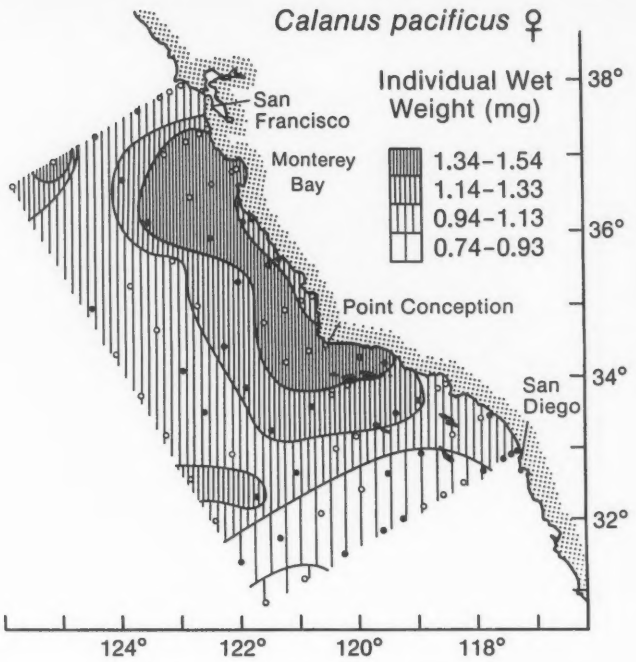

FIGURE 12.—*Calanus pacificus* females. Average individual wet weight in mg.

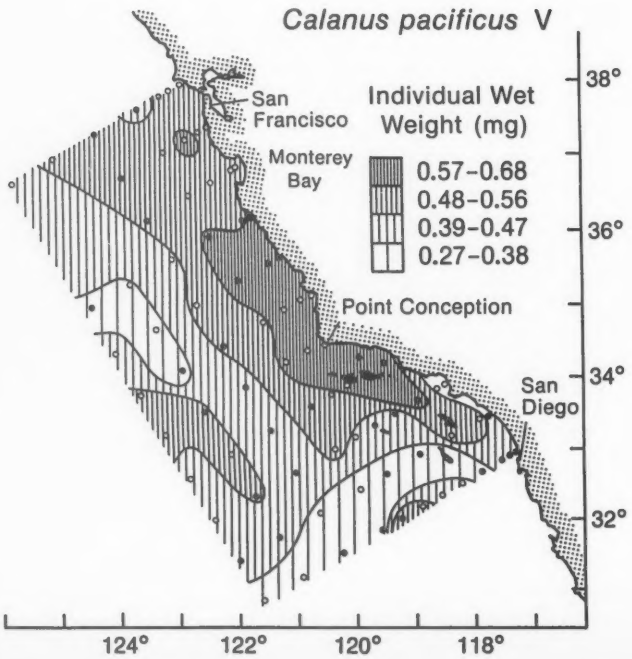

FIGURE 13.—*Calanus pacificus* Stages V copepodites. Average individual wet weight in mg.

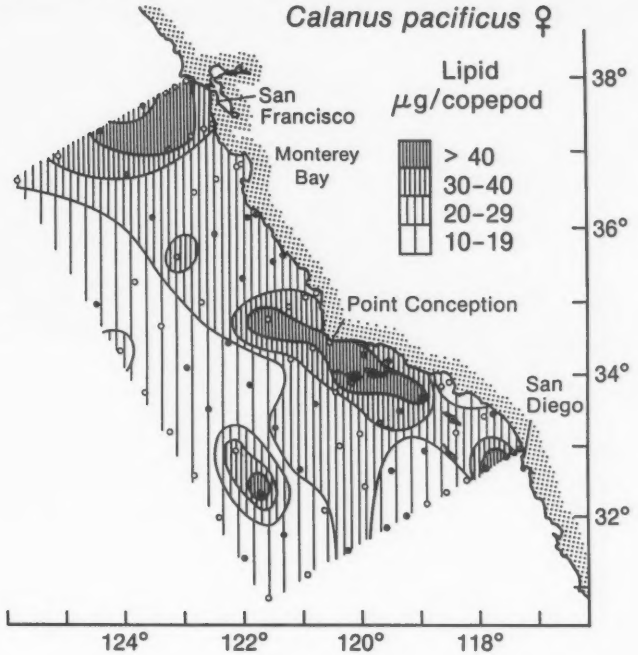

FIGURE 14.—*Calanus pacificus* females. Average lipid content per copepod in μg.

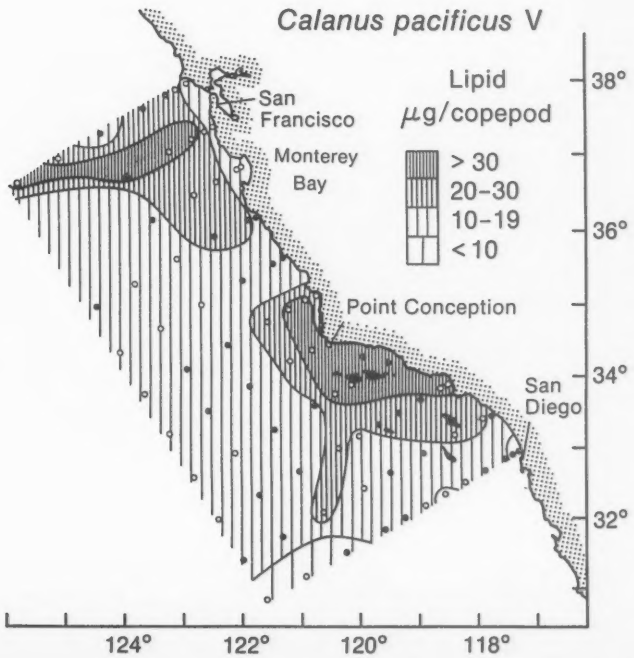

FIGURE 15.—*Calanus pacificus* Stage V copepodites. Average lipid content per copepod in μg.

Lipid content of female *C. pacificus*, expressed as percent dry weight or percent wet weight, was lowest in the southern offshore region, but was quite similar between the other three regions (Table 7). Lipid content (percent dry or wet weight) of stage V copepodites from the northern nearshore region was higher than the other regions. This stage showed the lowest lipid content in the southern offshore region (Table 7).

DISCUSSION

Upwelling was taking place along the California coast during April 1981. The resulting coastal low surface water temperatures were most evident in the northern part of the sampling grid, especially just north of Point Conception. An upwelling index calculated for this region during mid-April was higher than the 20-yr mean (Howe et al. 1981). The cold-water plume extending into the Southern California Bight (Fig. 2) is a common phenomenon that occurs when cold, upwelled water from the Point Conception region becomes entrained into the southward flowing California Current (Reid et al. 1958; Bernstein et al. 1977; Lasker et al. 1981). The distribution of phytoplankton biomass (estimated by surface chlorophyll a) was the most obvious biological feature associated with coastal upwelling. Phytoplankton patchiness in turn influenced zooplankton biomass and nutritional parameters. The following discusses 1) the relationships between various biological properties influenced by upwelling and 2) the persistence and consequences of biological mesoscale patchiness within the California Current System.

The distributions and abundances of both euphausiid species were similar to previous reports (Brinton 1962, 1967b, 1976, 1981; Brinton and Wyllie 1976; Youngbluth 1976). *Euphausia pacifica* is generally more abundant than *Nematoscelis difficilis*, and the center of its distribution is located closer to the coast. The abundance of *E. pacifica* within the sampling grid was positively correlated with phytoplankton biomass, as has been noted by Youngbluth (1976). Other herbivorous euphausiids (e.g., *Thysanoessa raschii* and *T. inermis*) also show this same relationship (Sameoto 1976).

The distribution and abundance of *Calanus pacificus* stages were also similar to previous reports (Fleminger 1964; Longhurst 1967). Both females and stage V copepodites were most abundant close to the coast near upwelling regions. In contrast to *E. pacifica*, abundances of the two *C. pacificus* stages showed rather poor (but significant at 95% level) correlations with phytoplankton biomass (r values of 0.24 and 0.31). This result was surprising since both species are considered herbivores. The weak correlations between *C. pacificus* abundance and phytoplankton standing crop probably resulted from small-scale heterogeneity and poor mobility of the *C. pacificus* population. Populations of *C. pacificus* along the California coast show a great deal of small-scale patchiness on the order of 10's to 100's of meters (Mullin and Brooks 1976; Star and Mullin 1981; Cox et al. 1982). Grazing by copepods within these patches can greatly reduce the local phytoplankton standing crop. When samples are taken on scales of 1 km or less, a poor or inverse correlation between phytoplankton and zooplankton biomass results (Mackas and Boyd 1979; Star and Mullin 1981). Zooplankton samples in this study were collected from net tows that covered distances of about 1 km or less. Thus, the poor correlations in the present study confirm results of previous studies and can be explained on the basis of the sampling procedure.

Laminarinase activity (LA) of *C. pacificus* and *E. pacifica* was positively related to phytoplankton standing crop. However, a strong relationship between these variables did not exist for either species (correlation coefficients between 0.53 and 0.62). These results were expected because, although most studies agree that zooplankton digestive enzyme activity and feeding rates are closely linked, enzyme levels do not always represent instantaneous ingestion rates nor are they always related to the food environment at the time of collection (Head and Conover 1983; Hassett and Landry 1983; Head et al. 1984; Willason and Cox in press).

We propose three, non-exclusive explanations for the observed weak correlations between LA and phytoplankton biomass. First, time lags of 1 to 7 d in the response of zooplankton digestive enzymes to changing food concentrations (Mayzaud and Poulet 1978; Cox and Willason 1981; Willason 1983) can influence the association between enzyme levels and the food environment. Because the standing stock of phytoplankton is often very patchy and can change rapidly, especially in upwelling regions, zooplankters are probably continually acclimating to new conditions and an equilibrium may seldom be reached between enzyme activity, feeding rates, and food concentration.

Second, phytoplankton concentration may occasionally be high in terms of chlorophyll a, but poor in quality resulting in low consumption rates and low digestive enzyme activity. Herbivorous zooplankton feeding rates have been shown to be greatly de-

pressed by the presence of unpalatable or toxic phytoplankton (Fielder 1982).

Third, recent evidence indicates that zooplankton digestive enzymes do not show a substrate-specific response. Head and Conover (1983) found that LA in *C. hyperboreus* was induced in animals which were fed an algae that did not contain laminarin. Willason (1983) found that levels of laminarinase in *E. pacifica* increased when animals consumed small, nonreactive charcoal particles. This increase in activity, however, was less than that of animals given phytoplankton as a food source. Hence, some types of nonphytoplankton food, such as detrital particles or fecal pellets, may also elicit a positive digestive enzyme response. However, since *E. pacifica* and *C. pacificus* are primarily herbivorous and are found close to the coast where phytoplankton is abundant, LA of these zooplankters is probably, for the most part, controlled by phytoplankton consumption.

Because of large-scale patchiness within the sampling grid, relationships between the various biological properties are much clearer when stations were grouped and regions or mesoscale features compared. Mesoscale patches (100 to 200 km) of *C. pacificus* and *E. pacifica* with high LA values were clearly associated with areas of highest phytoplankton standing crop: south of San Francisco Bay and particularly in the area adjacent to and just south of Point Conception. Although laminarinase levels may not always accurately represent the feeding conditions at a single station (because of the reasons stated above), large-scale comparisons indicate that digestive enzyme levels of herbivorous zooplankton are stongly influenced by overall food concentration within an area. This suggests that animals near the coastal upwelling regions were feeding at higher rates than animals from other areas of the sampling grid.

In contrast to *E. pacifica*, neither the abundance nor the LA of *N. difficilis* were correlated with phytoplankton standing crop. These differences between the two euphausiid species are due most likely to different feeding modes or different food preferences. *Nematoscelis difficilis*, unlike *E. pacifica* and *C. pacificus*, is probably not a herbivore. Nemoto (1967) concluded that its mouthparts were very different from those of most herbivorous euphausiids, and Willason and Cox (in press) found that phytoplankton was only a small part of the diet of *N. difficilis*. What is puzzling, however, are the high levels of LA we sometimes found in *N. difficilis*, a range of values similar to those of *E. pacifica*. Laminarinase levels in *N. difficilis* are apparently controlled by consumption of a food source other than phytoplankton. Since we did not examine the gut contents of *N. difficilis* nor quantify potential food other than phytoplankton, the type of food eaten by *N. difficilis* could not be determined.

Based on the weight and biochemical composition of *C. pacificus*, the areas of high feeding activity along the California coast appear to have been persistent for periods of at least 1 to 2 wk. *Calanus pacificus* from the northern nearshore region and from the area near Point Conception were heavier, had a lower water content, and a higher lipid content than copepods from other areas. This indicates that these copepods have had prolonged exposure to better feeding conditions. The use of zooplankton biochemical composition and weight as indices of relative "physiological" or "nutritional" state has been documented in laboratory experiments. Vidal (1980) showed a direct relationship between food concentration and weight of adult and stage V *C. pacificus*. Since *C. pacificus* completes a life cycle in about 30 d (Vidal 1980; Huntley and Brooks 1982) and has a fixed number of molts to maturity, 1 or 2 wk at higher food concentrations can have a large impact on adult size. The lipid content of a zooplankton species represents an energy reserve and is an excellent indicator of nutritional state. Lipid content increases in well-fed animals and decreases in starved animals (Lee et al. 1970, 1971; Mayzaud 1976; Hakanson 1984). During periods of starvation, crustaceans in the laboratory also show an increase in water content (Hiller-Adams and Childress 1983).

Two field studies have shown that changes in food quality and quantity can cause physiological or nutritional changes in zooplankton populations (Omori 1970; Boyd et al. 1978). In both of these cases, zooplankters were displaced from their optimal habitat to areas of lower food concentration by currents or eddies. The displaced zooplankters showed a lower lipid content and a higher water content presumably due to suboptimal nutrition. This may be what happened to individuals of *C. pacificus* in the offshore areas of the California Current. These copepods weighed less and were in poorer physiological condition (high water content and low lipid content) than *C. pacificus* located close to the upwelling regions. Although the origins of these copepods are not known, physical processes within the California Current System such as eddy extensions (Bernstein et al. 1977; Pelaez and Guan 1982; Haury 1984) or offshore surface transport mechanisms (Parrish et al. 1981) could displace zooplankters such as *C. pacificus* to the food-poor offshore waters.

Because euphausiids were captured at only about

one-half of the stations, comparisons of weight and water content between specific regions were difficult. Although the average weight of adults of both euphausiid species were greater in the northern area (nearshore and offshore combined), water content of both species was similar in all areas. The weight and biochemical composition of adult euphausiids may be less susceptible to short-term changes in food concentration than copepods because of their larger size and longer life cycle (>1 yr, Ross 1982).

Thus far, it is apparent that processes which occur in relatively small areas along the California coast, in particular the area near Point Conception, have a considerable influence on the nutritional state of two common herbivorous zooplankters, *E. pacifica*, and *C. pacificus*. What are the long-term implications of this mesoscale patchiness?

The regions of high phytoplankton standing crop found in April 1981 appear to be relatively predictable from year to year. Although upwelling events in these areas are episodic and seasonal, previous studies have shown similar patterns. CalCOFI surveys (Owen 1974) and recent satellite imagery (Smith and Baker 1982; Pelaez and Guan 1982) indicate that in past years Point Conception and the area off Monterey Bay have consistently been regions of high phytoplankton production during the spring and summer months. This enhanced production has undoubtedly influenced zooplankton populations in preceding years in much the same way that was found during the present study. Previous investigations concerning zooplankton distributions and grazing activity along the California coast support this conclusion (Fleminger 1964; Brinton 1976, 1981; Cox et al. 1982, 1983).

Although reproduction was not estimated, it is likely that well-fed zooplankters in the California Current produce more eggs than poorly fed animals. This has clearly been demonstrated in the laboratory for copepods (Marshall and Orr 1955; Checkley 1980) and has been suggested for euphausiids (Brinton 1976). Larger individuals of a species also produce more eggs (Brinton 1976; Nemoto et al. 1972; Ross et al. 1982). Thus, the larger, better fed copepods and euphausiids near Point Conception and off Monterey Bay probably have a higher reproductive output than animals from other areas. There is some evidence which suggests that enhanced reproduction of zooplankton takes place near Point Conception. Arthur (1977) noted that the highest densities of copepod nauplii in the Southern California Bight were located in a cold-water upwelling plume extending south from Point Conception. In addition, eggs and larvae of *E. pacifica* are more abundant in the Southern California region following periods of upwelling (Brinton 1976).

In summary, our results show that upwelling and phytoplankton variability have a significant impact on the herbivorous zooplankton in the California Current. Not only did we find patchiness of zooplankton abundances, but more importantly, zooplankton nutritional states were also highly variable (i.e., mesoscale and larger scale patchiness of trophic interactions). Zooplankton in upwelling regions appear to experience better feeding conditions for periods of up to several weeks. Prolonged periods of better feeding conditions in specific areas should influence secondary production as well. This implies that the relatively small, productive regions along the California coast, south of San Francisco Bay and particularly the area near Point Conception, have a disproportionally large impact on the biology of marine organisms within the California Current System.

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LITERATURE CITED

AUTHUR, D. K.
1977. Distribution, size, and abundance of microcopepods in the California Current system and their possible influence on the survival of marine teleost larvae. Fish. Bull., U.S. 75:601-611.

BAMSTEDT, U.
1975. Ecological aspects of individual variations in weight and protein and lipid content of *Euchaeta norvegica* (copepoda). Sarsia 59:31-46.

BERNSTEIN, R. L., L. BREAKER, AND R. WHRITNER.
1977. California Current eddy formation: ship, air, and satellite results. Science 195:353-359.

BLIGH, E. G., AND W. J. DYER.
1959. A rapid method of total lipid extraction. Can. J. Biochem. Physiol. 37:911-917.

BOYD, S. H., P. H. WIEBE, AND J. L. COX.
1978. Limits of *Nematoscelis megalops* in the northwestern Atlantic in relation to Gulf Stream cold core rings. II. Physiological and biochemical effects of expatriation. J. Mar. Res. 36:143-159.

BRINTON, E.
1962. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr., Univ. Calif. 8:51-270.

1967a. Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr. 12:451-483.

1967b. Distributional atlas of Euphausiacea (Crustacea) in the California Current region, Part I. Calif. Coop. Oceanic Fish. Invest. Atlas, Vol. 5, 275 p.

1976. Population biology of *Euphausia pacifica* off southern California. Fish. Bull., U.S. 74:733-762.

1981. Euphausiid distributions in the California Current during the warm winter-spring of 1977-78, in the context of a 1949-1966 time series. Calif. Coop. Oceanic Fish. Invest. Rep. 22:135-154.

BRINTON, E., AND A. W. TOWNSEND.

1981. A comparison of euphausiid abundances from bongo and 1-m nets. Calif. Coop. Oceanic Fish. Invest. Rep. 22:111-125.

BRINTON, E., AND J. G. WYLLIE.

1976. Distributional atlas of euphausiid growth stages off southern California, 1953-1956. Calif. Coop. Oceanic Fish. Invest. Atlas Vol. 24, 289 p.

CHECKLEY, D. M., JR.

1980. The egg production of a marine planktonic copepod in relation to its food supply: Laboratory studies. Limnol. Oceanogr. 25:430-446.

CHILDRESS, J. J.

1977. Physiological approaches to the biology of midwater organisms. *In* N. R. Andersen and B. J. Zahuranec (editors), Oceanic sound scattering prediction, Vol. 5, p. 301-324. Plenum Press, N.Y.

CHILDRESS, J. J., AND M. NYGAARD.

1974. Chemical composition and buoyancy of midwater crustaceans as a function of depth of occurrence off Southern California. Mar. Biol. (Berl.) 27:225-238.

COX, J. L.

1981. Laminarinase induction in marine zooplankton and its variability in zooplankton samples. J. Plankton Res. 3:345-356.

COX, J. L., L. R. HAURY, AND J. J. SIMPSON.

1982. Spatial patterns of grazing-related parameters in California coastal surface waters, July 1979. J. Mar. Res. 40:1127-1153.

COX, J. L., AND S. W. WILLASON.

1981. Laminarinase induction in *Calanus pacificus*. Mar. Biol. Lett. 2:307-311.

COX, J. L., S. W. WILLASON, AND L. HARDING.

1983. Consequences of distributional heterogeneity of *Calanus pacificus* grazing. Bull. Mar. Sci. 33:213-226.

FIEDLER, P. C.

1982. Zooplankton avoidance and reduced grazing responses to *Gymnodinium splendens* (Dinophyceae). Limnol. Oceanogr. 27:961-965.

FLEMINGER, A.

1964. Distributional atlas of calanoid copepods in the California Current region, Part I. Calif. Coop. Oceanic Fish. Invest. Atlas, Vol. 2, 313 p.

HAKANSON, J. L.

1984. The long and short term feeding condition in field-caught *Calanus pacificus*, as determined by the lipid content. Limnol. Oceanogr. 29:794-804.

HASSETT, R. P., AND M. R. LANDRY.

1982. Digestive carbohydrase activities in individual marine copepods. Mar. Biol. Lett. 3:211-221.

1983. Effects of food-level acclimation on digestive enzyme activities and feeding behavior of *Calanus pacificus*. Mar. Biol. (Berl.) 75:47-55.

HAURY, L. R.

1982. Mesoscale processes: The biological and physical connections. [Abstr.] EOS 63-68. Trans. Am. Geophys. Union.

1984. An offshore eddy in the California Current System Part IV: Plankton distributions. Prog. Oceanogr. 13:95-111.

HAURY, L. R., J. A. MCGOWAN, AND P. H. WIEBE.

1978. Pattern and processes in the time-space scales of plankton distributions. *In* J. H. Steele (editor), Spatial patterns in plankton communities, p. 277-327. Plenum Press, N.Y.

HAYWARD, T. L., AND E. L. VENRICK.

1982. Relation between surface chlorophyll, integrated chlorophyll and integrated primary production. Mar. Biol. (Berl.) 69:247-252.

HEAD, E. J. H., AND R. J. CONOVER.

1983. Induction of digestive enzymes in *Calanus hyperboreus*. Mar. Biol. Lett. 4:219-231.

HEAD, E. J. H., R. WANG, AND R. J. CONOVER.

1984. Comparison of diurnal feeding rhythms in *Temora longicornis* and *Centropages hamatus* with digestive enzyme activity. J. Plankton Res. 6:543-551.

HILLER-ADAMS, P., AND J. J. CHILDRESS.

1983. Effects of prolonged starvation on O_2 consumption, NH_4^+ excretion, and chemical composition of the bathypelagic mysid *Gnathophausia ingens*. Mar. Biol. (Berl.) 77: 119-127.

HOWE, J. T., D. B. GIBSON, T. O. EVANS, L. BREAKER, R. C. WRIGLEY, AND W. W. BROENKOW.

1981. Biological and physical oceanographic observations pertaining to the trawl fishery in a region of persistent coastal upwelling. NASA Tech. Mem. 81332.

HUNTLEY, M., AND E. R. BROOKS.

1982. Effects of age and food availability on diel vertical migration of *Calanus pacificus*. Mar. Biol. (Berl.) 71:23-31.

LASKER, R.

1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453-462.

LASKER, R., AND P. E. SMITH.

1977. Estimation of the effects of environmental variations on the eggs and larvae of the northern anchovy, *Engraulis mordax*. Calif. Coop. Oceanic Fish. Invest. Rep. 19:128-137.

LASKER, R., AND J. R. ZWEIFEL.

1978. Growth and survival of first-feeding northern anchovy larvae (*Engraulis mordax*) in patches containing different proportions of large and small prey. *In* J. H. Steele (editor), Spatial pattern in plankton communities, p. 329-354. Plenum Press, N.Y.

LASKER, R., J. PELÀEZ, AND R. M. LAURS.

1981. The use of satellite infrared imagery for describing ocean processes in relation to spawning of the northern anchovy (*Engraulis mordax*). Rem. Sens. Environ. 11:439-453.

LEE, R. F., J. C. NEVENZEL, G. A. PAFFENHOFER, AND A. A. BENSON.

1970. The metabolism of wax esters and other lipids by the marine copepod, *Calanus helgolandicus*. J. Lipid Res. 11: 237-240.

LEE, R. F., J. HIROTA, AND A. M. BARRETT.

1971. Distribution and importance of wax esters in marine copepods and other zooplankton. Deep-Sea Res. 18:1147-1165.

LONGHURST, A. R.

1967. Diversity and trophic structure of zooplankton communities in the California Current. Deep-Sea Res. 14:393-408.

LORENZEN, C. J.

1970. Surface chlorophyll as an index of the depth, chlorophyll content, and primary productivity of the euphotic layer. Limnol. Oceanogr. 15:479-480.

LYNN, R. J., K. A. BLISS, AND L. E. EBER.
1982. Vertical and horizontal distributions of seasonal mean temperature, salinity, sigma-t, dynamic height, oxygen, and oxygen saturation in the California Current, 1950-1978. Calif. Coop. Oceanic Fish. Invest. Atlas, Vol. 30, 513 p.

MACKAS, D. L., AND C. BOYD.
1979. Spectral analysis of zooplankton spatial heterogeneity. Science 204:62-64.

MARSH, J. B., AND D. B. WEINSTEIN.
1966. Simple charring method for determination of lipids. J. Lipid Res. 7:574-576.

MARSHALL, S. M., AND A. P. ORR.
1955. The biology of a marine copepod, *Calanus finmarchicus*. Oliver and Boyd., Edinb., 188 p.

MAUCHLINE, J., AND L. R. FISHER.
1969. The biology of euphausiids. Adv. Mar. Biol. 7:1-454.

MAYZAUD, P.
1976. Respiration and nitrogen excretion of zooplankton. IV. The influence of starvation on the metabolism and the biochemical composition of some species. Mar. Biol. (Berl.) 37:47-58.

MAYZAUD, P., AND S. A. POULET.
1978. The importance of the time factor in the response of zooplankton to varying concentrations of naturally occurring particulate matter. Limnol. Oceanogr. 23:1144-1154.

MERCHANT, D. J., R. H. KAHN, AND W. H. MURPHY, JR.
1964. Handbook of cell and organ culture. Burgess Publ., Minneap., 269 p.

MULLIN, M. M., AND E. R. BROOKS.
1976. Some consequences of distributional heterogeneity of phytoplankton and zooplankton. Limnol. Oceanogr. 21:784-796.

NEMOTO, T.
1967. Feeding pattern of euphausiids and differentiations in their body characteristics. Inf. Bull Planktol. Jpn, Commem. No. Y. Matusue, p. 157-171.

NEMOTO, T., K. KAMADA, AND K. HARA.
1972. Fecundity of a euphausiid crustacean, *Nematoscelis difficilis*, in the North Pacific Ocean. Mar. Biol. (Berl.) 14:41-47.

O'CONNELL, C. P.
1980. Percentage of starving northern anchovy, *Engraulis mordax*, larvae in the sea as estimated by histological methods. Fish. Bull., U.S. 78:475-489.

OMORI, M.
1970. Variations of length, weight, respiration rate, and chemical composition of *Calanus cristatus* in relation to its food and feeding. *In* J. H. Steele (editor), Marine food chains, p. 113-126. Oliver and Boyd, Edinb.

OWEN, R. W., JR.
1974. Distribution of primary production, plant pigments, and secchi depth in California Current 1969. Calif. Coop. Oceanic Fish. Invest. Atlas 20:98-117.
1980. Eddies of the California Current system: physical and ecological characteristics. *In* D. M. Power (editor), The California Islands: Proceedings of the Multidisciplinary Symposium, p. 237-263. Santa Barbara Mus. Nat. Hist.

PARRISH, R. H., C. S. NELSON, AND A. BAKUN.
1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175-203.

PELÆEZ, J., AND F. GUAN.
1982. California Current chlorophyll measurements from satellite data. Calif. Coop. Oceanic Fish. Invest. Rep. 23: 211-225.

REID, J. L., G. I. RODEN, AND J. G. WYLLIE.
1958. Studies on the California Current system. Calif. Coop. Oceanic Fish. Invest. Rep. 6:27-57.

ROSS, R. M.
1982. Energetics of *Euphausia pacifica* I. Effects of body carbon and nitrogen and temperature on measured and predicted production. Mar. Biol. (Berl.) 68:1-13.

ROSS, R. M., K. L. DALY, AND T. S. ENGLISH.
1982. Reproductive cycle and fecundity of *Euphausia pacifica* in Puget Sound, Washington. Limnol. Oceanogr. 27:304-314.

RYTHER, J. H.
1969. Photosynthesis and fish production in the sea. Science 166:72-76.

SAMEOTO, D. D.
1976. Distribution of sound scattering layers caused by euphausiids and their relationships to chlorophyll a concentrations in the Gulf of St. Lawrence Estuary. J. Fish. Board Can. 33:681-687.

SMITH, R. C., AND K. S. BAKER.
1982. Oceanic chlorophyll concentrations as determined by satellite (Nimbus-7 coastal zone color scanner). Mar. Biol. (Berl.) 66:269-279.

STAR, J. L., AND M. M. MULLIN.
1981. Zooplankton assemblages in three areas of the North Pacific as revealed by continuous horizontal transects. Deep-Sea Res. 28A:1303-1322.

STEELE, J. H.
1978. Some comments on plankton patches. *In* J. H. Steele (editor), Spatial patterns in plankton communities, p. 1-20. Plenum Press, N.Y.

STRICKLAND, J. D. H., AND T. R. PARSONS.
1972. A practical handbook of seawater analysis. Fish. Res. Board Can., Bull. 167, 310 p.

TORRES, J. J., AND J. J. CHILDRESS.
1983. The relationship of oxygen consumption to swimming speed in *Euphausia pacifica* I. Effects of temperature and pressure. Mar. Biol. (Berl.) 74:79-86.

VIDAL, J.
1980. Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. Mar. Biol. (Berl.) 56:111-134.

WILLASON, S. W.
1983. Spatiotemporal patterns of grazing and laminarinase activity of zooplankton off the California coast. Ph.D. Thesis, Univ. of California, Santa Barbara, 176 p.

WILLASON, S. W., AND J. L. COX.
In press. Diel feeding, laminarinase activity, and phytoplankton consumption by euphausiids. Biol. Oceanogr.

YOUNGBLUTH, M. J.
1976. Vertical distribution and diel migration of euphausiids in the central region of the California Current. Fish. Bull., U.S. 74:925-936.

RHIZOCEPHALAN INFECTION IN BLUE KING CRABS, *PARALITHODES PLATYPUS*, FROM OLGA BAY, KODIAK ISLAND, ALASKA

P. T. JOHNSON,[1] R. A. MACINTOSH,[2] AND D. A. SOMERTON[3]

ABSTRACT

An isolated population of blue king crabs, *Paralithodes platypus*, in Olga Bay, Kodiak Island, was sampled quarterly during 1980-81. It was found to contain abnormal mature females with degenerate ovaries and/or no sign of having extruded ova following molt. Histological studies of these females and of males and females collected subsequently in April 1982 showed that rhizocephalan internas (roots) were present in up to 50% of the population. Both males and females were infected, but male gonads and secondary sexual characteristics were apparently unaffected. Presence of the rhizocephalan was strongly related to ovarian abnormalities. Evidence suggests that infected females can molt, but do not extrude or retain embryos. The Olga Bay rhizocephalan is not related to *Briarosaccus callosus*, which parasitizes several species of Alaskan king crabs, including the blue king crab. Externas of the Olga Bay parasite were not found. The possible relationship of this rhizocephalan to the genus *Thompsonia*, which has minute multiple externa that might be missed during gross examination, and the possibility that the blue king crab is an abnormal host that does not allow development of externas are discussed.

Molting, mating, and extrusion of ova occur annually in red king crabs, *Paralithodes camtschatica*, and biennially in blue king crabs, *P. platypus*. Because embryos of both species hatch within about 1 yr, empty embryo cases are carried on blue king crabs in the second year (Powell and Nickerson 1965; Sasakawa 1973, 1975; Somerton and MacIntosh in press). Somerton and MacIntosh (1982)[4] studied an isolated population of blue king crabs in Olga Bay (Kodiak Island, AK) and found abnormal females that were of mature size but lacked external evidence of having extruded eggs or that had apparently degenerate ovaries. This paper reports results of gross and histological examination of blue king crabs from the aberrant Olga Bay population and from three apparently normal eastern Bering Sea populations. A rhizocephalan, which was found only in the Olga Bay crabs, appears to be responsible for the abnormal reproductive pattern.

MATERIALS AND METHODS

Blue king crabs in Olga Bay were sampled quarterly: spring (March-April 1980), summer (June 1980), autumn (October 1980), and winter (January 1981). Seasonal sample sizes ranged from 155 to 229 crabs, and a total of 422 males and 337 females was examined. Both sexes were measured to the nearest millimeter in carapace length (see Wallace et al. 1949, for measurement). Carapace lengths ranged from 12 to 162 mm for males and 16 to 143 mm for females. Data were taken on external egg clutches of females by relative volume, color of embryos, and presence or absence of eyespots on embryos. Presence or absence of empty embryo cases on nonovigerous females was also noted.

For the purposes of this paper, "oogonia" are stem cells; "oocytes" are developing cells before full maturity; and "ova" are cells that have completed vitellogenesis, have a thick chorion, and are ready for fertilization. "Embryo" refers to an external, fertilized, and developing egg or ovum.

The entire ovary and a pleopod with attached embryos or empty embryo cases (if present) were removed from each female considered to be mature or in the prepubertal stadium (>68 mm carapace length (CL)). These were preserved in 10% freshwater (river water) Formalin[5] solution buffered with sodium

[1]Northeast Fisheries Center Oxford Laboratory, National Marine Fisheries Service, NOAA, Oxford, MD 21654.

[2]Northwest and Alaska Fisheries Center Kodiak Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 1638, Kodiak, AK 99615.

[3]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way, N.E., Seattle, WA 98115.

[4]Somerton, D. A., and R. A. MacIntosh. 1982. Aspects of the life history of the blue king crab (*Paralithodes platypus*) in Alaska. Document submitted to the annual meeting of the International North Pacific Fisheries Commission, Tokyo, Japan, October 1982.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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borate (10 g/L solution). The wet weight of preserved ovaries was recorded to the nearest g and diameters of a sample of oocytes/ova were recorded to the nearest 0.1 mm using a stereomicroscope.

Because many of the ovaries appeared abnormal and could not be classified easily by oogenetic stage, histological examination was undertaken of ovaries and pleopods from the largest sample, collected in January 1981 (Table 1). To provide material for a more detailed examination, the Olga Bay population was sampled again in April 1982, and three apparently normal Bering Sea populations of blue king crabs were also sampled (Table 1). Except as indicated, tissues taken in these collections included portions of the central nervous system, gut, hepatopancreas, gills, eyestalks, epidermis, heart, antennal gland, bladder, ovary, female pleopods, anterior vas deferens, and, in some cases, testis and hemopoietic tissue.

Except for the January samples from Olga Bay (fixed in borate Formalin), all tissues were fixed in Helly's solution (containing zinc chloride rather than mercuric chloride) for 3-4 d, washed 1-2 h in 50% ethyl alcohol, and stored in 70% ethyl alcohol until being processed by standard histological methods.

To provide a basis for comparison, ovaries and pleopods of 11 female red king crabs collected at Olga Bay, January 1981, and fixed in borate Formalin, and tissues from two blue king crabs collected at Glacier Bay, AK, infected with the rhizocephalan *Briarosaccus callosus*, and fixed in Helly's solution, were also prepared for histological examination.

RESULTS

Prevalence of the Rhizocephalan

The roots (internas) of a rhizocephalan were associated with either or both the ovary and the pleopod in 52% of the 104 blue king crab females taken from Olga Bay in January 1981, and with various tissues in 40% of the 15 females and 33% of the 15 males taken from Olga Bay in April 1982 (Table 2). The rhizocephalan was also found in 1 of the 11 red king

TABLE 1.—Origins of blue king crabs examined histologically.

Location	Date	Number of specimens	Carapace length (mm)
Olga Bay	8-14 Jan. 1981	104 females (ovaries and pleopods)	69-136
Olga Bay	5-9 Apr. 1982	15 males	88-151
		15 females	90-128
Pribilof Is.	25 June-3 July 1982	10 males	83-155
		10 females (plus ovaries and pleopods from an additional 10 females)	96-145
Pribilof Is.	21 Feb. 1983	10 females	113-137
St. Matthew I.	10-13 July 1983	17 males	68-158
		9 females	61-129
St. Lawrence I.	5-11 Sept. 1982	5 males	85-106
		5 females	79-104

TABLE 2.—Rhizocephalans in individual male and female blue king crabs, Olga Bay, Kodiak Island, AK, April 1982.

			Major areas parasitized (in tissue sections)					
Sex	Intensity of infection	Degenerate roots	Nerve cord, assoc. bladder	Bladder in other areas	Gut	Gonad	Antennal gland	Hepato-pancreas
Female	±[1]		+[2]					
	+		+	+	+	+	+	+
	+	+[3]	+	+	+			
	++	+	+			+		
	++	+	+	+	+	+		+
	+++	+	+	+		+	+	+
Male	±			+				
	+		+		+			+
	+	+	+	+	+			+
	++	+	+	+	+		+	+
	++	+	+	+	+	+	+	+

[1] ± = light infection; + to +++ = medium to very heavy infection.
[2] + = parasite present.
[3] + = present.

crab females taken from Olga Bay in January 1981. Rhizocephalan externas were never detected. Rhizocephalan tissue was not found in any of the 76 blue king crabs collected from the Bering Sea and examined by us.

Data on females collected from Olga Bay in January 1981 and April 1982 were combined and then separated into various categories of reproductive condition, based on both histological condition and reproductive features of the ovary and on external reproductive features. Females in all categories were further classified by the presence or absence of rhizocephalan infection, as determined histologically (Table 3).

The effect of the rhizocephalan on female reproduction was examined by testing the independence of probable future reproductive success and rhizocephalan presence. Based on ovarian categories (Table 3), probable future reproductive success was judged as either successful (no degenerating gonadal cells) or unsuccessful (ovary empty or ovary with degenerate gonadal cells). Independence of probable future success and rhizocephalan presence was rejected for both measures, implying that rhizocephalan infestation significantly reduces the probability of future reproductive success ($\chi^2 = 16.81$, df = 1, $P < 0.001$ for empty ovary; $\chi^2 = 20.41$, df = 1, $P < 0.001$ for ovary with degenerate gonadal cells).

Three of the external categories of females (Table 3) represent crabs at different times after extrusion of ova. Embryos begin to develop eyes about 4 mo after extrusion. Hatching occurs slightly more than 12 mo after extrusion. Following hatching, empty embryo cases persist on the pleopod setae until the crab molts again, usually slightly <12 mo later (Somerton and MacIntosh in press). Therefore, the generalized time since extrusion for the uneyed, eyed, and empty-embryo-case categories is 0-4 mo, 4-14 mo, and 14-24 mo, respectively. If parasitic attacks are random and prevent successful extrusion and embryo attachment, then prevalence of the parasite should be low for females with uneyed embryos and should increase with time. Independence between prevalence and time since extrusion (using uneyed and empty-embryo-case categories) was rejected ($\chi^2 = 7.79$, df = 1, $P < 0.01$).

TABLE 3.—Prevalence of rhizocephalan infection in female blue king crabs (>68 mm CL) collected in Olga Bay, Kodiak Island, AK, January 1981 and April 1982.

	Parasitized		Not parasitized
	n	%	
Ovarian categories			
Ovary empty	15	71	6
Ovary with gonadal cells[1]			
With some degenerate cells	38	64	21
No degenerate cells	7	18	32
External categories			
Clean pleopod setae	19	51	18
Ovigerous			
Uneyed embryos	1	10	9
Eyed embryos	12	48	13
Previously ovigerous (embryo cases)	27	59	19

[1]Oocytes and/or ova.

Females are grasped by males and held in a "precopulatory embrace" before molting and mating. Of the 10 grasped females collected January 1981, 5 showed no evidence of previous reproductive activity, and 5 had empty embryo cases. None were infected with the rhizocephalan, although three of the females with empty embryo cases had some degenerate gonadal cells.

Based on the April 1982 sample, which includes males, independence between sex and rhizocephalan presence was not rejected ($\chi^2 = 0.14$, df = 1, $P = 0.75$). The rhizocephalan, therefore, does not appear to discriminate by host sex.

Presence of the rhizocephalan apparently did not affect the gonads of males. Both infected and noninfected males had numerous spermatophores in the anterior vas deferens. Spermatocytes, some of them dividing, and developing and mature sperm were present in the four crabs whose testes were sampled (one parasitized and three nonparasitized). In the field, we saw no males exhibiting female secondary sexual characteristics.

Histological Observations

Rhizocephalan roots occupied the hemal spaces of the pleopods, were associated with the exterior of the ovary, and occasionally lay within internal hemal spaces of the ovary of infected females collected in January 1981. Roots were associated with various tissues of males and females collected from Olga Bay in April 1982 (Table 2). Hemal sinuses of the ovary and those abutting the gut, the bladder, and the thoracic ganglia were the most frequently invaded sites. Roots lay within the glia of the thoracic ganglia of one crab, but otherwise were confined to hemal spaces and did not invade tissues.

Roots were cylindrical and surrounded by a PAS-positive cuticle of variable thickness (Figs. 1, 3). Cells within the roots usually had large vesicular nuclei, and refractile spherules were sometimes present in the cytoplasm. Usually the roots were tubular, with a defined lumen, and those with large, empty lumens often had a flattened epithelium. Loosely anasto-

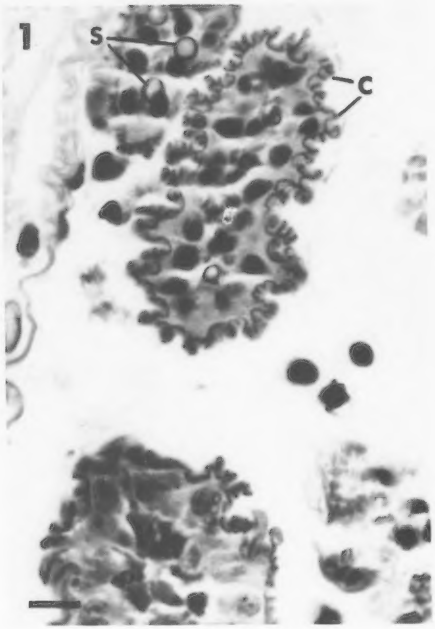


FIGURE 1.—Olga Bay rhizocephalan: Cross sections of roots with occluded lumens. PAS. C, cuticle; S, refractile cytoplasmic spherules. Bar = 10 μm.

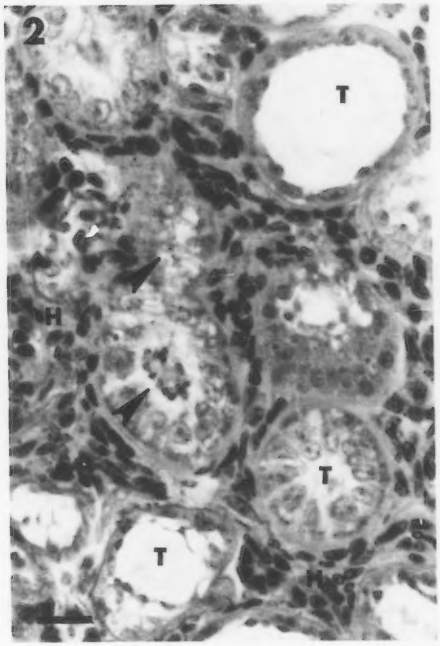


FIGURE 2.—Olga Bay rhizocephalan: Normal roots, lying in an area invaded by hemocytes. Note variable size of the lumen and one tubule with a group of small, central nuclei and another with anastomosing cells in the lumen (arrows). PAS. H, hemocytes; T, tubular roots. Bar = 20 μm.

mosing cells filled the lumen of some tubules, and a defined epithelium was not present in these (Fig. 2). Roots with narrow or occluded lumens often had smaller, denser nuclei in the epithelium, or an additional interior layer or group of cells with small, dense, or condensed nuclei (Fig. 2). The occluded roots may represent the distal, growing portions of the organism.

Intensity of infection varied (Table 3). In all of the heavier infections and most of the medium ones, portions of the roots were degenerate or necrotic (Fig. 3). Host hemocytes had aggregated in such areas and often had encapsulated the degenerate roots. In heavy infections with many degenerating and necrotic roots, blackened areas, probably due to melanin deposition in the roots, were visible with the naked eye in the tissues. Sometimes hemocytes had invaded the lumens of degenerate and necrotic roots, and other roots had been reduced to amorphous material surrounded by hemocytes (Fig. 3). In all cases, roots of normal appearance were also present in the same areas. In only one instance were normal roots surrounded by hemocytes (Fig. 2). Probably the section had been cut just peripherally to a large area of degenerating roots.

Ovaries of 88% (53/60) of parasitized females as opposed to 46% (27/59) of normal females either contained no oocytes or had some or all degenerate oocytes (Fig. 4). Figure 5 shows a normal ovary with previtellogenic oocytes. Grasped females all had normal oocytes that were in late vitellogenesis and enclosed by a thick chorion. Of the 10 grasped females, 9 were in the premolt condition, and the 10th, a precocious juvenile 77 mm CL, was in the intermolt.

None of the parasitized crabs were in advanced premolt, although some were judged to be in early premolt because the pleopod epidermis was thickened, and occasionally a developing epicuticle was present.

Excepting the ovary, tissues and organs appeared normal in the parasitized crabs. Whether or not there was reduced lipid storage in the hepatopancreas was not evident by histological examination of the present series.

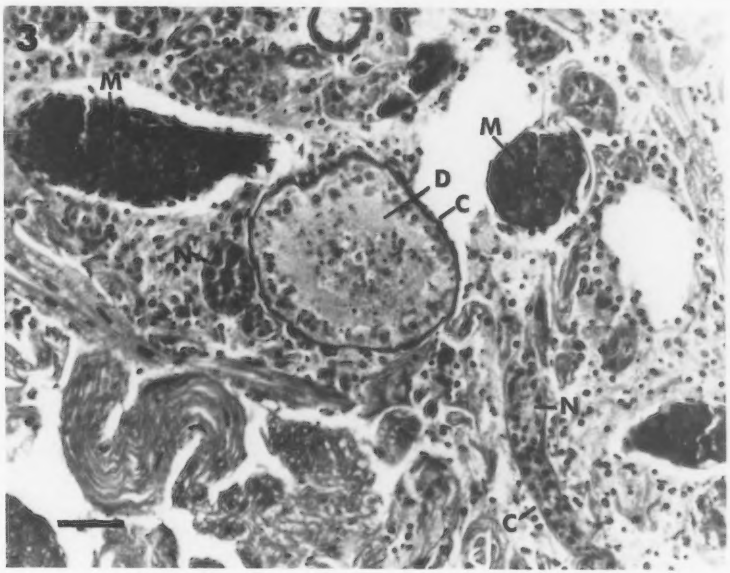
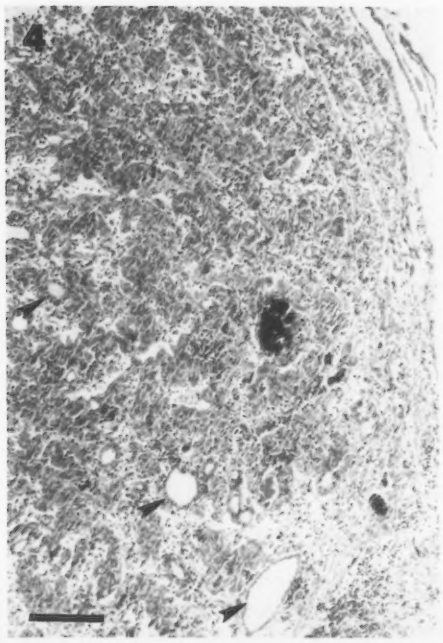


FIGURE 3.—Olga Bay rhizocephalan: Degenerating and normal roots. PAS. N, normal tubule; C, cuticle; D, tubules with sloughing epithelium; M, completely necrotic tubule; H. hemocytes. Bar = 0.05 mm.



DISCUSSION

The presence of the rhizocephalan in female blue king crabs appears to impair reproductive function. Most parasitized crabs have empty ovaries or ovaries that contain degenerate gonadal cells. We assume that these traits are linked to reproductive failure, although there are also unparasitized crabs within each category. It is not unusual to find a few retained ova—destined to be resorbed—in a normal post-extrusion ovary. Therefore, these crabs are also a source of degenerate gonadal cells. The 2-yr reproductive cycle of the blue king crab might also lead to presence of degenerate gonadal cells that had been produced early in the cycle and had become senescent. This speculation remains to be investigated.

The increase in the incidence of infection over time in postextrusion crabs also suggests reproductive impairment. Not only is the prevalence very low (10%) among females that had recently extruded (with uneyed embryos), it is zero among grasped premolt females that were presumably about to molt, mate,

FIGURE 4.—Olga Bay rhizocephalan: Empty ovary of an infected crab. Arrows point to roots of the parasite. PAS. Bar = 0.2 mm.

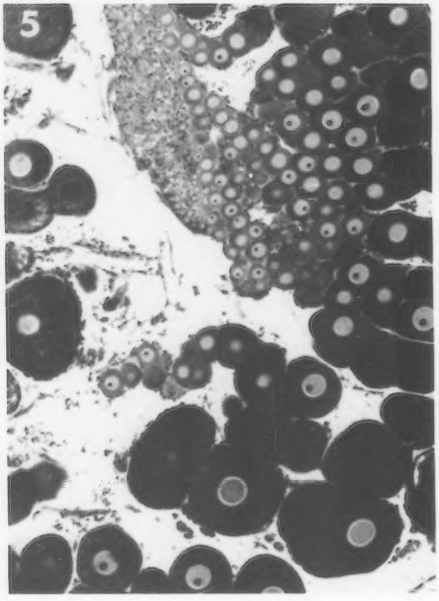


FIGURE 5.—Normal ovary with oogonia and previtellogenic oocytes. PAS. Same scale as Fig. 4.

and extrude. These facts suggest that the rhizocephalan might preclude mating and subsequent extrusion and attachment of fertilized ova.

The external category of reproductive condition we term "clean pleopod setae" would normally be associated with immature crabs. In this study, it contained both small females and females of mature size (total size range 69-133 mm CL). The average size at maturity of females in Alaskan populations lacking the rhizocephalan ranges from 80 to 96 mm (Somerton and MacIntosh 1983). Crabs larger than 114 mm could reasonably be expected to be carrying embryos or empty embryo cases, but 10 crabs in the combined January-April sample (9 of which had the rhizocephalan) were not. Two of the parasitized females were soft-shelled, suggesting that molting can occur in parasitized females.

Presence of the rhizocephalan in male crabs from Olga Bay apparently did not interfere with normal gonadal function. Species of *Sacculina* and many other rhizocephalans cause a varying degree of external feminization and gonadal dysfunction of their male hosts (Reinhard 1956). For example, *Thompsonia mediterranea* causes external appendages of males of *Callianassa truncata* to approach the female condition (Caroli 1931), but a species of *Thompsonia* parasitizing *Portunus pelagicus* does not affect males (Phang 1975). *Briarosaccus callosus* parasitizes the blue, red, golden (*Lithodes aequispina*), and deep-sea (*Lithodes couesi*) king crabs in the Gulf of Alaska (McMullen and Yoshihara 1970; Somerton 1981; Hawkes et al. 1985). Meyers[6] found testicular regression and broadening of the abdomen in *Briarosaccus*-infected male blue king crabs from Glacier Bay.

High prevalences of infection with rhizocephalans have been reported previously in other decapod species, so the high prevalence in blue king crabs of Olga Bay is not surprising. McMullen and Yoshihara (1970) found 14 of 21 golden king crabs, captured near Kodiak Island, infected with *B. callosus*, and Hawkes et al. (1985) reported 76% prevalence of the same species in blue king crabs from Glacier Bay; Phang (1975) reported prevalences between 24% and 68% of *Thompsonia* sp. in groups of *Portunus pelagicus* captured near Singapore; and Perry (1984) said that sometimes over 50% of blue crabs sampled from a single population in the Gulf of Mexico were infected with *Loxothylacus texanus*.

Although nearly 800 blue king crabs were sampled from Olga Bay at quarterly intervals, no rhizocephalan externas were observed, and the one red king crab female found infected with what appeared to be the same rhizocephalan also lacked an externa. Due to the absence of externas, the Olga Bay rhizocephalan cannot be indentified with certainty. Its roots are similar histologically to those of other rhizocephalans [*Thompsonia* (Potts 1915); *Sacculina* (Fischer 1927; Dornesco and Fischer-Piette 1931); and *Peltogaster* and *Gemmosaccus* (Nielsen 1970)], corresponding best with the roots of *Thompsonia*, which have a thinner cuticle than the others (Potts 1915). Roots of the Olga Bay parasite differ histologically in several ways from those of *Briarosaccus callosus*. They are of lesser diameter, have a thinner cuticle, lack large peripheral nuclei, often have a large lumen and flattened epithelium, and seldom have the cytoplasmic vacuoles (probably representing lipid storage) that are common in the *B. callosus* roots. (Compare Figures 1, 2, and 3 with Figure 6.) The Olga Bay parasite and *B. callosus* also differ in that the roots of *B. callosus* are a bright green when fresh (Hawkes et al. 1985) and blue-green when fixed in Helly's solution, whereas the roots of the Olga Bay parasite are colorless.

[6]T. Meyers, Assistant Professor of Fisheries, School of Fisheries and Science, University of Alaska, 11120 Glacier Highway, Juneau, AK 99801, pers. commun. October 1984.

The lack of obvious externas on the parasitized crabs is puzzling. One possibility is that externas are produced but are inconspicuous and/or evanescent. Most rhizocephalans produce easily detected externas that emerge from the venter of the abdomen. Species of *Thompsonia*, however, produce multiple small externas 1-4.5 mm long and no more than 1.1 mm in diameter. These externas occur on the appendages and venters of the thorax and abdomen, depending on the species, and those of at least one of the species are easily dislodged (Häfele 1911; Potts 1915; Phang 1975). If few and scattered externas of the *Thompsonia* type were present, they could have escaped notice on animals as large as the blue king crabs investigated. The second possibility is that externas are not developed in the blue king crab. Host ranges of rhizocephalans are often broad, but some of the host/parasite associations may be accidental or not fully evolved. *Sacculina carcini* is known to react differently in different species of crabs. In *Carcinus maenas* multiple broods of larvae are produced by *S. carcini*, but if the host is *Portunus holsatus*, it breeds but once and then is shed, which suggests that *C. maenas* is a natural host but *P. holsatus* is an adventitious and not entirely competent one (Baer 1951). Perhaps the Olga Bay parasite is not a usual parasite of the blue king crab, and although the interna develops extensively and causes severe damage to female gonads, externas cannot be produced in this species. The fact that some roots of the parasite were degenerating or necrotic in most infected crabs suggests that parasites do die within the blue king crab, and that infections might be lost before externas are formed.

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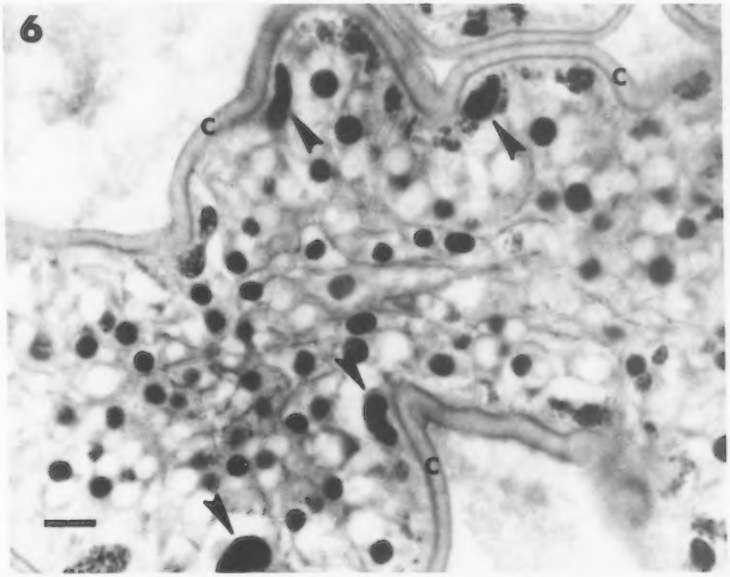

FIGURE 6.—*Briarosaccus callosus*: Roots. Note lack of a central lumen and the very large, peripheral nuclei (arrows). Feulgen. C, cuticle. Bar = 10 μm.

LITERATURE CITED

BAER, J. G.
1951. Ecology of animal parasites. Univ. Illinois Press, Urbana, IL, 224 p.

CAROLI, E.
1931. Azione modificatrice dei Bopiridi e dei Rizocefali sui caratteri sessuali secondarii delle Callianasse. Arch. Zool. Ital. 16:316-322.

DORNESCO, G. T., AND E. FISCHER-PIETTE.
1931. Données cytologiques sur les "racines" de la Sacculine, Crustacé parasite. Bull. Histol. Appl. 8:213-221.

FISCHER, E.
1927. Sur le tissu constituant les "racines" endoparasitaires de la Sacculine. C. R. Soc. Biol. 96:329-330.

HÄFELE, F.
1911. Anatomie und Entwicklung eines neuen Rhizocephalen: *Thompsonia japonica*. Beiträge zur Naturgeschichte Ostasiens. Abh. bayer. Akad. Wiss. Math.-phys. Kl., Suppl.-Bd. 2, Abh. 7, p. 1-25.

HAWKES, C. R., T. R. MEYERS, AND T. C. SHIRLEY.
1985. Parasitism of the blue king crab, *Paralithodes platypus*, by the rhizocephalan, *Briarosaccus callosus*. J. Invertebr. Pathol. 45:252-253.

MCMULLEN, J. C., AND H. T. YOSHIHARA.
1970. An incidence of parasitism of deepwater king crab, *Lithodes aequispina*, by the barnacle *Briarosaccus callosus*. J. Fish. Res. Board Can. 27:818-821.

NIELSEN, S.-O.
1970. The effects of the rhizocephalan parasites *Peltogaster paguri* Rathke and *Gemmosaccus sulcatus* (Lilljeborg) on five species of paguridan hosts (Crustacea Decapoda). Sarsia 42:17-32.

PERRY, H. M.
1984. A profile of the blue crab fishery of the Gulf of Mexico. Gulf States Mar. Fish. Comm., Spec. Publ. 9, 80 p.

PHANG, V. P. E.
1975. Studies on *Thompsonia* sp. a parasite of the edible swimming crab *Portunus pelagicus*. Malay. Nat. J. 29:90-98.

POTTS, F. A.
1915. On the rhizocephalan genus *Thompsonia* and its relation to the evolution of the group. Pap. Dep. Mar. Biol. Carnegie Inst. Wash. 8:1-32.

POWELL, G. C., AND R. B. NICKERSON.
1965. Reproduction of king crabs, *Paralithodes camtschatica* (Tilesius). J. Fish. Res. Board Can. 22:101-111.

REINHARD, E. G.
1956. Parasitic castration of Crustacea. Exp. Parasitol. 5: 79-107.

SASAKAWA, Y.
1973. Studies on blue king crab resources in the western Bering Sea. I. Spawning cycle. [In Jpn.] Bull. Jpn. Soc. Sci. Fish. 39:1031-1037. (Engl. transl. NOAA Lang. Serv. Branch.)
1975. Studies on blue king crab resources in the Western Bering Sea. II. Verification of spawning cycle and growth by tagging experiments. [In Jpn.] Bull. Jpn. Soc. Sci. Fish. 41: 937-940. (Engl. transl. NOAA Lang. Serv. Branch.)

SOMERTON, D. A.
1981. Contribution to the life history of the deep-sea king crab *Lithodes couesi*, in the Gulf of Alaska. Fish. Bull., U.S. 79: 259-269.

SOMERTON, D. A., AND R. A. MACINTOSH.
1983. The size at sexual maturity of blue king crab, *Paralithodes platypus*, in Alaska. Fish. Bull., U.S. 81:621-628.

SOMERTON, D. A., AND R. A. MACINTOSH.
In press. Reproductive biology of the blue king crab, *Paralithodes platypus*, in the eastern Bering Sea. J. Crustacean Biol.

WALLACE, M. M., C. J. PERTUIT, AND A. H. HVATUM.
1949. Contributions to the biology of the king crab *Paralithodes camtschatica* (Tilesius). U.S. Fish Wild. Serv., Fish. Leafl. 340, 49 p.

NOTES

THE SEX RATIO AND GONAD INDICES OF SWORDFISH, *XIPHIAS GLADIUS*, CAUGHT OFF THE COAST OF SOUTHERN CALIFORNIA IN 1978

In the tropical and subtropical Pacific, swordfish, *Xiphias gladius*, about to spawn are found throughout the year but are most abundant from March to July (Palko et al. 1981). There is, however, little information on the reproductive potential of swordfish during their summer and autumn migrations into the Southern California Bight, a temperate region encompasing the principal U.S. west coast swordfish fishing grounds. In 1978 scientists from the Southwest Fisheries Center collected the gonads of swordfish harpooned in the Bight (from Point Conception to the United States-Mexico border) in order to determine sex ratios, gonad indices, and the reproductive condition of these fish.

Methods

Ninety swordfish were sampled from 25 August through 20 November 1978. After capture their gonads were preserved in 10% Formalin[1] and, in the laboratory, were weighed to the nearest gram and their sex determined visually. Ovarian sections used in the histological analysis were obtained from segments removed from the centers of the ovaries. Segments were imbedded in Paraplast and 8 μm sections were cut, stained in iron hematoxylin, and counterstained in eosin.

Two gonad indices were calculated for each pair of ovaries to permit comparisons with two existing studies on the sexual maturity of Pacific swordfish. The first (from Uchiyama and Shomura 1974) is simply the percentage of the fresh weight of the ovaries to the total weight of the fish:

$$GI = \frac{WT\text{-}O}{WT\text{-}F} \times 100 \qquad (1)$$

where GI = gonad index,
$WT\text{-}O$ = fresh weight of both ovaries, and
$WT\text{-}F$ = fresh weight of whole fish.

The second index (from Kume and Joseph 1969) is

$$GI = (W/L^3) \times 10^4 \qquad (2)$$

where GI = gonad index,
W = fresh weight of both ovaries in grams, and
L = post-orbital fork length in centimeters.

Because the gonads used in this study were preserved, and thus subject to shrinkage and loss of weight, it was necessary to estimate their fresh weight using the relationship (from Uchiyama and Shomura 1974):

$$Y = e^{\frac{\ln X - 0.155}{0.969}} \qquad (3)$$

where Y = estimated fresh weight of ovaries, and
X = weight of preserved ovaries.

The estimated weight loss due to preservation was as high as 7%.

Results and Discussion

All 90 swordfish collected were mature with fork lengths ranging from 133 to 218 cm. Of these, 23 (26%) were males and 67 (74%) were females for a sex ratio of 0.34:1 (M:F). Although the proportion of females varied among months, our sample sizes were too small to demonstrate such variation.

Female swordfish in our sample all had gonad indices that were considerably lower than those of comparable studies. Uchiyama and Shomura (1974) collected 16 pairs of ovaries from swordfish caught near Hawaii and found three pairs to be ripe. These had gonad indices (from Equation (1)) of 6.4, 8.4, and 9.8 whereas our highest value (from Equations (1) and (3)) was 1.0. Kume and Joseph (1969) examined 362 pairs of ovaries from swordfish captured in the eastern Pacific (east of long. 130°W) and found two ripe specimens whose gonad indices (from Equation (2)) were 10.8 and 11.1. By comparison, the highest from our study (from Equations (2) and (3)) was 1.8. These results indicate swordfish in the Southern California Bight during our sampling period were not spawning.

A histological analysis was performed on a subset of 16 pairs of ovaries from our sample. Histological analyses can be used to determine not only if a fish

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

is in spawning condition but, also, if it has recently spawned (Hunter and Macewicz 1985). Ovaries from our sample contained no mature oocytes and, in addition, did not contain abundant atretic oocytes indicative of the resorption process. Instead the ovaries were in the regressed stage and contained primary oocytes lining connective tissue septa. These results indicate that the swordfish were reproductively inactive during the sampling period and for at least a month or two before capture. Although this conclusion does not preclude the possibility of spawning early in the year, swordfish then are scarce. Also water temperatures favorable for spawning (Palko et al. 1981) are not widespread in the summer and autumn, and are virtually nonexistant the remainder of the year.

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Literature Cited

HUNTER, J. R., AND B. J. MACEWICZ.
1985. Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 83:119-136.

KUME, S., AND J. JOSEPH.
1969. Size composition and sexual maturity of billfish caught by the Japanese longline fishery in the Pacific Ocean east of 130 W. Bull. Far Seas Fish. Res. Lab. (Shimizu) 2:115-162.

PALKO, B. J., G. L. BEARDSLEY, AND W. J. RICHARDS.
1981. Synopsis of the biology of the swordfish, *Xiphias gladius* Linnaeus. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 441, 21 p.

UCHIYAMA, J. H., AND R. S. SHOMURA.
1974. Maturation and fecundity of swordfish, *Xiphias gladius*, from Hawaiian waters. *In* R. S. Shomura and F. Williams (editors), Proceedings of the International Billfish Symposium Kailua-Kona, Hawaii, 9-12 August, 1972. Part 2. Review and contributed papers, p. 142-148. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF 675.

EARL C. WEBER

Southwest Fisheries Center La Jolla Laboratory
National Marine Fisheries Service, NOAA
8604 La Jolla Shores Drive
La Jolla, CA 92038

STEPHEN R. GOLDBERG

Department of Biology
Whittier College
Whittier, CA 90608

GROWTH OF DOLPHINS, *CORYPHAENA HIPPURUS* AND *C. EQUISELIS*, IN HAWAIIAN WATERS AS DETERMINED BY DAILY INCREMENTS ON OTOLITHS

The dolphin, *Coryphaena hippurus*, and pompano dolphin, *C. equiselis*, are widely distributed pelagic fishes in tropical and subtropical oceans (Beardsley 1967; Rose and Hassler 1968; Shcherbachev 1973). In Hawaiian waters *C. hippurus* is caught throughout the year, but its abundance fluctuates. Small fish (<2.3 kg) are plentiful in summer and large fish (13.6-18.1 kg) are more abundant from February to April (Squire and Smith 1977). *Coryphaena hippurus* is important to the commercial and recreational fisheries; *C. equiselis*, a smaller fish with a maximum length of 74 cm (Herald 1961), is occasionally caught by recreational fishermen. Although much is known about the life history of *C. hippurus* in the Atlantic (Palko et al. 1982), the biology of the Hawaiian population has been only sketchily investigated. Little is known about *C. equiselis*.

At least three age and growth studies on *C. hippurus* have been reported. Annual marks on scales have been used to age *C. hippurus* off Florida (Beardsley 1967) and North Carolina (Rose and Hassler 1968) in the western North Atlantic Ocean. Wang (1979) used monthly modal progression of length-frequency distributions to estimate the growth rate of *C. hippurus* off eastern Taiwan in the western Pacific Ocean. The estimated growth rates of *C. hippurus* off Florida and North Carolina differed slightly, but the growth rate of *C. hippurus* in the western Pacific Ocean was reported to be about twice as great as those in the western North Atlantic Ocean.

The purpose of this study was to validate estimates of age and growth of larval and juvenile *C. hippurus* and *C. equiselis* based on microstructure of otoliths (sagittae) from fish of known age reared in captivity. Otoliths from wild specimens captured in Hawaiian waters were also used as a source of age and growth information and these data were fitted to the von Bertalanffy growth model. Ages of cultured and captured wild specimens were estimated by enumerating presumed daily increments on the sagitta following Pannella (1971). The daily nature of the increments was validated by counts from sagittae of fish reared in captivity and whose age was known. Knowledge of growth rates of both species of dolphins are useful to mariculturists who would like to compare the growth rates of wild and cultured individuals. Information on the growth rate of *C. hippurus* can also be of use to managers of Hawaiian fishery resources.

Materials and Methods

Validation

Fertilized eggs of *C. hippurus* and *C. equiselis* were obtained between January 1982 and February 1983 from captive broodstock held at the University of Hawaii's Waikiki Aquarium (WA); the Kewalo Research Facility (KRF) of the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service; and The Oceanic Institute, Waimanalo, HI. Larvae of both species were reared at the WA in 4,000 L circular fiber glass tanks with flow-through water exchange and under shaded natural light condition. Water temperature ranged between 23° and 27°C. Both species were fed an unlimited supply (a density of 1-5/mL) of cultured copepod, *Euterpina acutifrons*, and *Artemia* sp. until they were large enough to accept chopped fish and squid (about 30 d after hatching), which were then provided several times during the day. These fish were fed to satiation. One 167-d-old and three 191-d-old *C. hippurus* were reared at the KRF under similar environmental conditions and feeding regime as at the WA.[1] These juvenile *C. hippurus* were transferred to 8 m diameter tanks when they were about 25 cm long.

One to three larvae of *C. equiselis* were sampled on the day of hatching (D-0), and each day thereafter (D-1, D-2, D-4, etc.). However, after the fourth day, there were few survivors, so only a single specimen was taken at intervals of 4 d from D-19. Three larvae of *C. hippurus* were sampled on D-4 and single specimens were sampled at various intervals or obtained after accidental deaths for validating the growth increments. Other larvae were sampled from other batches on D-0, D-1, and D-2 for measurements. Specimens were sampled around noon. Total length of the larvae was measured under a microscope with an ocular micrometer while the specimen was alive or within an hour after death. To facilitate measurement, each larva was put on a glass slide, extended to its full length, and measured. For the examination of otoliths, the larva on the slide was immersed in 70% ethanol and allowed to fix for an hour. The larva was then removed from the ethanol bath, blotted, and mounted in Euparal,[2] a water soluble mounting medium, and covered with a cover slip. Otoliths could be examined in the squashed whole mount without extracting them.

After measuring the fork length of juvenile and adult dolphins with a caliper to the nearest millimeter, otoliths were extracted, cleaned, and mounted whole. To extract the otoliths, the head was removed from the body, and the flesh removed from the head to expose the skull. With a saw or knife, most of the supraoccipital and roof of the skull were removed. After careful removal of the brain, the sagittae (largest of the three otoliths) could be found in the sacculi located anteriorly on the right and left sides of the first vertebra at the caudal end of the brain cavity. Under a dissecting microscope, the sagitta was teased out of the sacculus, and extraneous tissues were brushed away. The pair of sagittae was then placed on a clean glass slide, permitted to dry, and mounted in Euparal. Segments of monofilament line slightly thicker than the sagittae were placed on both sides of the sagittae to prevent the cover slip from crushing it.

After clearing for a month, presumed daily increments on a sagitta were enumerated using a compound binocular microscope with transmitted light at 600× magnification. Increments were counted starting from the core out to the edge of the postrostrum, or from the core to the tip of the rostrum. Usually, counts could not be made in a direct line from the core to the edge of the rostrum or postrostrum of the sagitta; rather, a somewhat circuitous route was taken from one area of the sagitta to another by following a prominent growth increment. Increments were also counted inward from the edge to the core. Two independent age estimations were made separately on the rostrum and postrostrum on a sagitta to verify the age of fish. In some samples, it was possible only to make a single age estimate since the sagitta was incomplete, having just a rostrum or postrostrum. The reader had no information such as specimen size or previous counts to prevent bias in the counting.

The arithmetic mean of 3-14 counts was used to estimate a fish's age. The number of counts from the rostrum and postrostrum varied from as few as 3 for a larva to 14 for a sagitta of a juvenile. The relationship between counts of otolith increments and days was assessed for both species by regression analysis.

Growth of Wild Specimens

Juveniles of both species were dip netted from Kaneohe Bay, HI. Large juveniles and adults of both species were obtained from private and chartered

[1]Thomas K. Kazama, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812, pers. commun. October 1984.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

sport fishing boats in Honolulu, and *C. hippurus* specimens were also obtained from cruises of the NOAA ship *Townsend Cromwell* to the Northwestern Hawaiian Islands from October 1976 to September 1981. Fork lengths were measured to the nearest millimeter with calipers. The extraction and slide preparation of sagittae, and counting method were the same as described for the validation experiments above. But before reading the sagittae of fish caught in the wild, the sagitta of a known-age fish was re-examined to review the difference between known daily increments and subdaily increments. Concentric daily increments, which consist of an inner light band and an outer dark band, were distinguished from subdaily increments by carefully focusing to the plane of maximum clarity. The dark band of the subdaily increment appeared less defined than the dark band of daily increments. Misinterpretation and counting subdaily increments as daily increments could result in an overestimation of age. The mean of 10-20 counts was used as the age estimate of older fish.

Age estimates of wild fish were fitted to the von Bertalanffy growth model using NLIN Procedure, a nonlinear regression routine (SAS Institute 1982). The three juvenile *C. hippurus* whose sex was undetermined were added to both the male and female groups when fitting the curves.

Results

Validation

Fertilized eggs of *C. equiselis* and *C. hippurus* began to hatch after 48-50 h at 24°25°C and all hatched within 2 h. The larvae of both species were 4.0-4.6 mm TL and had two pairs of otoliths, the sagitta and lapillus, at time of hatching. Otoliths of *C. equiselis* and *C. hippurus* on D-0 ranged from 16 to 20 μm in diameter and consisted of the core and primordium. An hour after hatching, the larvae were from 5.2 to 5.4 mm TL but did not grow during the next 3 d and even shrank from 0.1 to 0.2 mm. Otoliths of both species on D-1 had a dark ring near the edge which the otoliths of D-0 larvae did not have and were 22-24 μm in diameter. The sagittae of both species on D-4 had four increments (Fig. 1) and were now slightly larger than the lapillus. Sagittal diameters were 29-36 μm for *C. equiselis* and 34-41 μm for *C. hippurus*.

Mean counts of growth increments on the sagittae of 10 *C. hippurus* (Table 1) and 13 *C. equiselis*

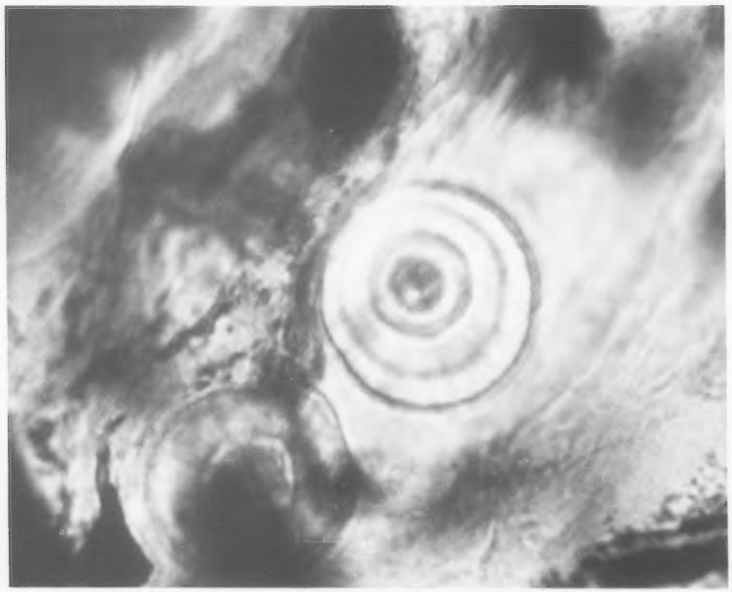


FIGURE 1.—Sagitta of a day-4 *Coryphaena hippurus* larva. Diameter of sagitta is 17 μm.

TABLE 1.—Mean of counts on known age sagittae of *Coryphaena hippurus*.

Known age	Mean increment counts	SD	No. of counts	Total length (mm)	Fork length (mm)
0	0			5.3	
1	1			—	
4	4	0.00	3	6.7	
4	4	0.00	3	6.8	
4	4	0.00	3	6.8	
20	20.0	±1.26	5	—	
35	33.6	±2.06	9	—	—
47	45.2	±3.16	10	—	95.0
167	166.8	±7.14	11	—	383.0
191	190.3	±6.92	6	—	510.0
191	191.0	±0.71	4	—	554.0
191	192.8	±7.44	5	—	491.0

TABLE 2.—Mean counts on known age sagittae of *Coryphaena equiselis*.

Known age	Mean increment counts	SD	No. of counts	Total length (mm)	Fork length (mm)
0	0			4.0	
1	1	0.00	3	—	
1	1	0.00	3	—	
4	3	0.00	3	4.6	
4	4	0.00	3	5.2	
19	19	0.00	3	14.2	
23	23.6	±2.23	8	23.0	
27	21.5	±1.59	14	25.2	
31	31.7	±1.38	7	—	29.5
36	35.3	±2.45	10	—	48.0
51	51.7	±2.13	13	—	82.0
52	53.6	±4.81	14	—	72.0
63	63.3	±3.19	14	—	89.0
63	63.4	±8.59	13	—	112.0

(Table 2) were plotted against corresponding known ages (Figs. 2, 3). The relationships of mean increment counts (Y) to known age (X) were $Y = -0.5295 + 1.0035X$ ($r = 0.999$, $P < 0.01$) for 10 *C. hippurus* and $Y = -0.6986 + 1.0164X$ ($r = 0.997$, $P < 0.01$) for 13 *C. equiselis*. These results demonstrated that growth increments are formed daily, and validated their use for aging wild fish up to 191 d for *C. hippurus* and 63 d for *C. equiselis*.

Growth of Wild Specimens

Because of sexual dimorphism, separate von Bertalanffy growth parameters were calculated for male and female *C. hippurus* (Table 3). The male and female von Bertalanffy growth curves and 18 age-length relationships of *C. hippurus* are shown in

TABLE 3.—Von Bertalanffy growth parameters calculated from captured wild specimens of *Coryphaena hippurus*.

Sex	Number	Parameter	Estimate	SE
Male	10	t_0	0.0790 yr	0.0305
		K	1.1871	0.5218
		L_∞	189.9301 cm FL	48.9702
Female	9	t_0	0.0731 yr	0.0126
		K	1.4110	0.2454
		L_∞	153.2676 cm FL	14.2168

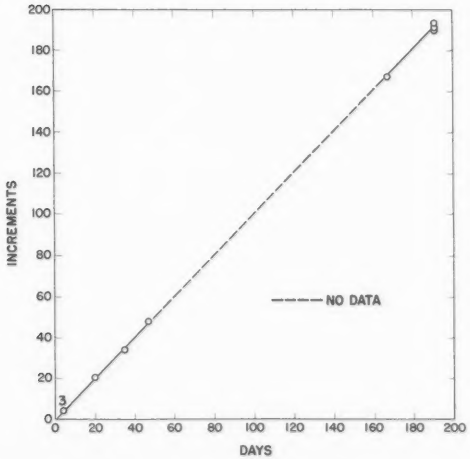


FIGURE 2.—Validation of daily increments on sagittae of *Coryphaena hippurus* by relationship of known age (X) to mean increment count (Y) up to 191 d ($r = 0.999$).

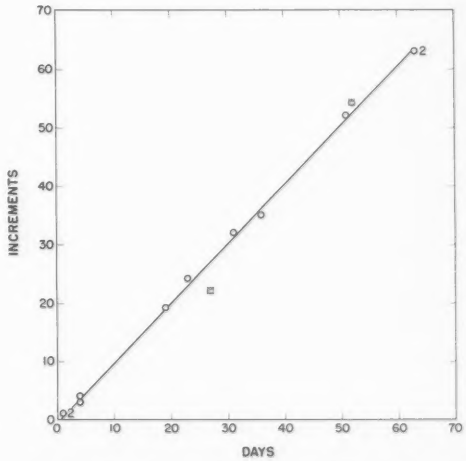


FIGURE 3.—Validation of daily increments on sagittae of *Coryphaena equiselis* by relationship of known age (X) to mean increment count (Y) up to 63 d ($r = 0.997$).

Figure 4. A single set of growth parameters (Table 4) was calculated for *C. equiselis* since the largest specimen in the sample had just reached sexual maturity, and the calculation of separate growth curves by sex was not warranted. The von Bertalanffy growth curve and 13 age-length relationships of *C. equiselis* are shown in Figure 5.

Discussion

Validation

A pair of otoliths was present at the time of hatching for both dolphins, and the first increment was formed on the otoliths on D-1, identical to *Katsuwonus pelamis*, another tropical pelagic species (Radtke 1983). The strong correlation of mean increment counts of sagittae to known age of fish validated the use of growth increments in the aging of *C. equiselis* up to 63 d and *C. hippurus* up to 191 d. Since regular incremental formation began on D-1, no adjustment is required to the incremental counts of wild fish sagittae to estimate age. Ideally, validation of daily increments should cover 1) the time when the first daily increment is formed, 2) the regularity in the formation of increments in all stages of life, and 3) events such as spawning, migration, and periods of starvation which may affect the regularity of increment formation. Having achieved only part of these requirements, validation of daily increments on otoliths should continue as older known-age specimens become available, and the effects of spawning and starvation on increment formation should also be examined.

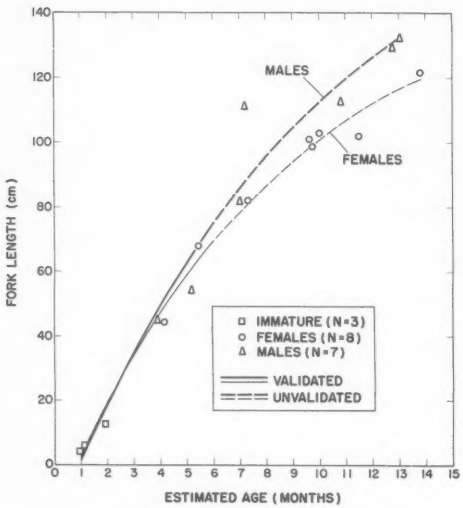


FIGURE 4.—Von Bertalanffy growth curves of male and female *Coryphaena hippurus* in Hawaiian waters.

TABLE 4.—Von Bertalanffy growth parameters calculated from captured wild specimens of *Coryphaena equiselis*.

Number	Parameter	Estimate	SE
13	t_0	0.0648 yr	0.0131
	K	2.1734	0.9750
	L_∞	61.3914 cm FL	17.8000

Growth of Wild Specimens

The plot of age-length relationships of male *C. hippurus* showed that there was at least one extreme variant. This 111.0 cm FL male greatly affected the growth curve, resulting in a lower estimated L_∞ and causing most of the male age estimates to fall below the growth curve (Fig. 4). Thus, age-length relations of wild *C. hippurus* should be examined further to shed light on the extent of variation in size at given ages. Additional age determinations might also improve the confidence intervals of the von Bertalanffy growth parameters.

Growth rates of *C. hippurus* to age 1 around Hawaii appeared to be greater than those reported from the western North Atlantic Ocean. Beardsley (1967) reported a mean length of 72.5 cm in age group 1 for *C. hippurus* off Florida. Rose and Hassler (1968) reported a mean length of 65.3 cm at the end of 1 yr for fish off North Carolina. Around Hawaii male *C. hippurus* were estimated to attain

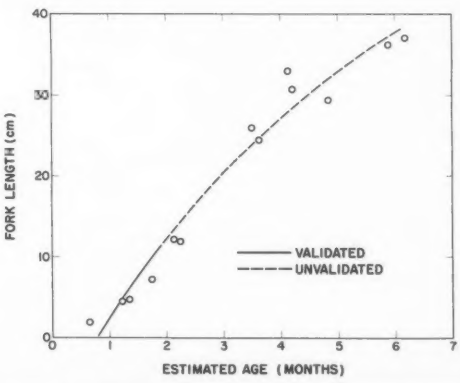


FIGURE 5.—Von Bertalanffy growth curve of *Coryphaena equiselis* in Hawaiian waters derived from 13 age estimates.

a length of about 126 cm at 1 yr and about 112 cm for females. The slower growth rate of *C. hippurus* in the western North Atlantic Ocean may be the result of a decrease in feeding rate when water temperature goes below 23.0°C and a cessation of feeding at 18.0°C (Hassler and Hogarth 1977). *Coryphaena hippurus* feed throughout the year in Hawaii and can be expected to grow continuously.

Wang (1979) used the monthly progression of modes in length-frequency distributions to estimate growth rates of about 10 cm/mo from February through June for *C. hippurus* between 50 and 100 cm FL. This growth rate is similar to that found for *C. hippurus* in Hawaiian waters.

Growth rates of captive *C. hippurus* were similar to those of wild fish in Hawaiian waters. Beardsley (1967) reported rapid growth rates of three captive *C. hippurus*. These fish grew from about 35 to 125 cm in 7 to 8 mo.[3] Soichi (1978) reported that 11 *C. hippurus* 35-50 cm TL grew to a mean 123 cm TL in 7-8 mo. Their observations also support our estimates of rapid growth for *C. hippurus* around Hawaii.

Coryphaena equiselis appeared to grow as rapidly as *C. hippurus* during the first 4 mo, then grew at a slower rate (Fig. 5). At about 4 mo, *C. equiselis* reached sexual maturity. *Coryphaena hippurus* also reached sexual maturity at 4-5 mo, but have been observed to mature as early as 3 mo in captivity.

The daily regularity of increment formation has been demonstrated from D-1 to D-191 for *C. hippurus* and from D-1 to D-63 for *C. equiselis*. So the use of daily increment counts on the sagitta of wild fish for estimating age has only been partially validated for these dolphins. The age-length relationships are valid for the first 6 mo for wild *C. hippurus* and the first 2 mo for wild *C. equiselis*. Thus, the von Bertalanffy growth curves calculated for wild *C. hippurus* in Hawaiian waters should be viewed with caution despite good agreement with several other growth observations in the literature.

Acknowledgments

Our thanks to Richard W. Brill, Richard E. Brock, Leighton R. Taylor, and Jerry A. Wetherall for their critical reviews of this manuscript. Carol Hopper greatly assisted our sampling efforts for wild-caught specimens and Thomas K. Kazama provided the oldest known-age *C. hippurus*.

[3]A length-weight relationship (Gibbs and Collette 1959) was used to estimate lengths in centimeters from weights, given in pounds, by Beardsley (1967).

Literature Cited

Beardsley, G. L., Jr.
1967. Age, growth, and reproduction of the dolphin, *Coryphaena hippurus*, in the Straits of Florida. Copeia 1967: 441-451.

Gibbs, R. H., Jr., and B. B. Collette.
1959. On the identification, distribution, and biology of the dolphins, *Coryphaena hippurus* and *C. equiselis*. Bull. Mar. Sci. Gulf Caribb. 9:117-152.

Hassler, W. W., and W. T. Hogarth.
1977. The growth and culture of dolphin, *Coryphaena hippurus*, in North Carolina. Aquaculture 12:115-122.

Herald, E. S.
1961. Living fishes of the world. Doubleday and Co., Inc., Garden City, NY, 304 p.

Palko, B. J., G. L. Beardsley, and W. J. Richards.
1982. Synopsis of the biological data on dolphin-fishes, *Coryphaena hippurus* Linnaeus and *Coryphaena equiselis* Linneaus. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 443, 28 p. [Also FAO Fish. Synop. 130.]

Pannella, G.
1971. Fish otoliths: Daily growth layers and periodical patterns. Science (Wash., D.C.) 173:1124-1127.

Radtke, R. L.
1983. Otolith formation and increment deposition in laboratory-reared skipjack tuna, *Euthynnus pelamis*, larvae. *In* E. D. Prince and L. M. Pulos (editors), Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks, p. 99-103. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8.

Rose, C. D., and W. W. Hassler.
1968. Age and growth of the dolphin, *Coryphaena hippurus* (Linnaeus), in North Carolina waters. Trans. Am. Fish. Soc. 97:271-276.

SAS Institute.
1982. SAS user's guide: Statistics. SAS Institute Inc., Cary, NC, 584 p.

Shcherbachev, Yu. N.
1973. The biology and distribution of the dolphins (Pisces, Coryphaenidae). [In Russ.] Vopr. Ikhtiol. 13:219-230. (Engl. transl. in J. Ichthyol. 13:182-191.)

Soichi, M.
1978. Spawning behavior of the dolphin, *Coryphaena hippurus*, in the aquarium and its eggs and larvae. [In Jpn., Engl. summ.] Jpn. J. Ichthyol. 24:290-294.

Squire, J. L., Jr., and S. E. Smith.
1977. Anglers' guide to the United States Pacific coast: marine fish, fishing grounds & facilities. U.S. Dep. Commer., NOAA, NMFS, 139 p.

Wang, C. H.
1979. A study of population dynamics of dolphin fish (*Coryphaena hippurus*) in waters adjacent to eastern Taiwan. [In Chin., Engl. abstr.] Acta Oceanogr. Taiwan. 10:233-251.

James H. Uchiyama

Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
P.O. Box, 3830, Honolulu, HI 96812

Raymond K. Burch
Syd A. Kraul, Jr.

Waikiki Aquarium, University of Hawaii
2777 Kalakaua Avenue
Honolulu, HI 96815

SIZES OF WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*, CONSUMED BY MARINE MAMMALS IN THE BERING SEA

In the Bering Sea at least 11 species of marine mammals, 13 seabirds, and 10 fishes are known to feed on walleye pollock, *Theragra chalcogramma* (Frost and Lowry 1981a). Walleye pollock are a major food of most pinnipeds, particularly in the southern Bering Sea (Lowry and Frost 1981), and are sometimes eaten by several species of baleen and toothed whales (Frost and Lowry 1981b).

In recent years, walleye pollock have been the principal target species in the Bering Sea commercial groundfish fishery. Annual catches have been as high as 1,840,000 t in 1972 (Bakkala et al. 1981). While there can be little doubt that both the fishery and marine mammal predation affect pollock stocks and perhaps also one another, the interactions are poorly understood at present (Lowry et al.[1]; Swartzman and Harr 1983).

An important aspect of marine mammal-fishery interactions is the size composition of fishes eaten in relation to that of the commercial catch. For example, if a marine mammal consumes fishes smaller than those taken by the fishery, the fishery would be unlikely to influence availability of food to the predator unless it affected recruitment. If marine mammals and the fishery remove fishes of similar sizes, competition would be expected (IUCN[2]).

Stomach contents of marine mammals seldom contain intact fishes in a condition suitable for measuring. However, the sagittal otoliths of species such as walleye pollock are easily identified (Frost 1981), and equations are available that estimate the length and weight of fishes from otolith lengths (Frost and Lowry 1981a). We present here information on the sizes of walleye pollock consumed by marine mammals in the Bering Sea, based on otoliths from gastrointestinal tracts.

Methods

Specimens were collected during the months of March to October 1975-81, at the locations shown in Table 1. With the exception of a minke whale, *Balaenoptera acutorostrata*, which was stranded on shore, all specimens were from animals collected for scientific purposes. Stomachs were removed and opened, and the contents gently washed on a 1 mm mesh sieve. Otoliths were sorted from other ingesta and identified using the descriptions of Morrow (1979) and Frost (1981). Since fresh walleye pollock otoliths have fine lobulations around their perimeter (Frost 1981) which disappear during digestion, degraded otoliths were easily detected by compari-

[1]Lowry, L. F., K. J. Frost, D. G. Calkins, G. L. Swartzman, and S. Hills. 1982. Feeding habits, food requirements, and status of Bering Sea marine mammals. North Pac. Fish. Manage. Counc. Doc. 19 and 19A, Anchorage, Alaska, Contract 81-4, 574 p.

[2]IUCN. 1981. Report of IUCN workshop on marine mammal-fishery interactions, La Jolla, Calif., 30 March-2 April. IUCN, Gland, Switzerland, 68 p.

TABLE 1.—Location and dates of capture of marine mammals from which otoliths of walleye pollock were obtained.

Species	Dates	Location	No. of specimens	No. of otoliths measured
Harbor seal, *Phoca vitulina richardsi*	13 Apr. 1979	Otter Island	4	23
	9 Oct. 1981	Port Heiden	1	12
Spotted seal, *Phoca largha*	6 May 1978	61°42.3N, 175°36.0W	1	11
	23 May 1978	63°25.8N, 173°05.6W	1	10
Ribbon seal, *Phoca fasciata*	19-20 Apr. 1976	57°20.1N-57°28.0N 172°30.9W-173°07.5W	5	256
	21-22 Mar. 1977	58°51.0N-58°56.0N 172°40.0W-173°08.0W	4	67
	5-31 May 1978	61°23.0N-64°39.4N 169°07.0W-176°08.8W	10	145
Steller sea lion, *Eumetopias jubatus*	20 Mar. 1976	56°04.8N, 168°32.9W	1	274
	13 Apr. 1979	Otter Island	1	6
	24 Mar., 10-11 Apr. 1981	59°30.0N-60°11.5N 176°43.5W-179°55.0W	32	497
	30 Mar.-4 Apr. 1981	59°08.0N-60°13.0N 165°45.0E-170°46.0E	56	638
Minke whale, *Balaenoptera acutorostrata*	5 Aug. 1975	Unalaska Island	1	121

son with those taken from trawl-caught fishes. The maximum length of nondegraded otoliths was measured to the nearest 0.1 mm using vernier calipers. When more than 20 otoliths occurred in a single stomach, a subsample of 20 was measured.

Very few otoliths were found in the stomachs of ribbon, *Phoca fasciata*, and spotted, *P. largha*, seals. For those species, additional otoliths were obtained from small intestines which were split along their entire length and examined for parasitological studies. There was no significant difference between sizes of otoliths obtained from stomachs and intestines of ribbon seals (Frost and Lowry 1980). Too few otoliths were retrieved from spotted seal stomachs to test their sizes relative to otoliths from intestines. However, otoliths from intestines were of the same general size range and condition as those from stomachs. We therefore pooled the measurements of otoliths from stomachs and intestines.

The fork lengths and weights of walleye pollock consumed were estimated from equations in Frost and Lowry (1981a).

Results

We measured a total of 2,060 otoliths from 117 individual marine mammals belong to 5 species (Table 1). Most of the otoliths were from the stomachs and small intestines of 19 ribbon seals and 90 Steller sea lions, *Eumetopias jubatus*. Ribbon seals, spotted seals, and a minke whale fed primarily on walleye pollock <20 cm long (Table 2, Fig. 1). Harbor seals, *Phoca vitulina richardsi*, fed on a wide size range of pollock, including equal numbers of fishes 8-15 cm and 20-35 cm long and a few individuals 45-56 cm in length. Most pollock eaten by sea lions (76%) were 20 cm or longer. Young sea lions (≤4 yr) collected in 1981 (all were males) ate significantly smaller fish ($\bar{x}$ = 22.4 cm, n = 37) than did older animals ($\bar{x}$ = 26.9 cm, n = 51; $P < 0.005$).

There were some differences in sizes of pollock consumed at different localities and in different years. The sizes of pollock eaten by harbor seals collected at Otter Island in 1979 ranged from 10.3 to 56.3 cm ($\bar{x}$ = 31.8 cm), while those eaten by a seal collected at Port Heiden in 1981 were all <12.6 cm long ($\bar{x}$ = 10.6 cm). Two sea lions collected in 1976 and 1979 near the Pribilof Islands had eaten pollock averaging 46.9 cm in length (range 18.4-61.4 cm), while those collected in 1981 to the west had eaten substantially smaller pollock averaging 25.2 cm in length (range 8.3-64.2 cm). In Figure 1, the smaller size mode corresponds to 1981 collections and the larger mode to those from 1976 and 1979. In 1981 sea lions collected in the central Bering had eaten larger pollock than those off the Kamchatka Peninsula ($\bar{x}$ = 26.8 cm vs. 23.5 cm; $P < 0.001$). This was not attributable to different age or size composition of the samples, since the difference was apparent for older sea lions (≥5 yr; $\bar{x}$ = 27.8 cm vs. 25.6 cm; $P < 0.01$) as well as the samples as a whole, and the mean age and standard length of all sea lions ≥5 yr in the Kamchatka sample ($\bar{x}$ age = 9.1 yr, $\bar{x}$ SL = 297 cm, n = 27) was greater than that of the central Bering sample ($\bar{x}$ age = 8.2 yr, $\bar{x}$ SL = 282 cm, n = 25).

Discussion

Of the marine mammal species we examined, ribbon seals, spotted seals, and a minke whale ate almost exclusively small pollock, whereas Steller sea lions and harbor seals ate pollock of a wide range of sizes. There are few other data available on the sizes of pollock consumed by marine mammals in the Bering Sea. Nemoto (1959) indicated that the length of pollock eaten by fin whales, *Balaenoptera physalus*, never exceeded 30 cm, while larger pollock were sometimes eaten by humpback whales, *Megaptera novaeangliae*. Fiscus et al. (1964) reported that in 1962 northern fur seals, *Callorhinus ursinus*, ate mostly whole pollock <30-35 cm long. McAlister et al.[3] found intact pollock in fur seal stomachs collected in the eastern Bering Sea, July-September 1974, to range from 10 to 35 cm, with a mean length of 19.3 cm. Most specimens were between 16 and 21 cm long. In 1981, Loughlin[4] collected fur seals north of Unalaska Island and found the average size of pollock consumed to be 30.4 cm. Antonelis[5] found that bearded seals, *Erignathus barbatus*, collected near St. Matthew Island in the central Bering Sea had eaten only small pollock ($\bar{x}$ length = 8.2 cm).

It is unknown whether the consumption patterns described above are a result of actual size selection of prey or if they result from coincidental distribution of predators and prey size classes. The overall density of pollock and distribution by age classes are far from uniform in the southern Bering Sea (Smith 1981; Bakkala and Alton[6]). The sizes of fishes con-

[3]McAlister, W. B., G. A. Sanger, and M. A. Perez. 1976. Preliminary estimates of pinniped-finfish relationships in the Bering Sea. Unpubl. background paper, 19th meeting North Pac. Fur Seal Comm., Moscow, 1976.

[4]T. R. Loughlin, National Marine Mammal Laboratory, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. commun. November 1983.

[5]G. Antonelis, National Marine Mammal Laboratory, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. commun. December 1983.

[6]Bakkala, R., and M. Alton. 1983. Evaluation of demersal trawl survey data for assessing the condition of eastern Bering Sea

TABLE 2.—Summary of sizes of walleye pollock consumed by marine mammals in the Bering Sea.

Marine mammal species	Size of walleye pollock consumed			
	Fork length		[1]Weight of mean length fish (g)	[1]Mean weight of fishes consumed (g)
	Mean (cm)	Range (cm)		
Ribbon seal	11.2	6.5-34.4	8.6	11.2
Spotted seal	10.9	8.0-15.0	7.9	8.4
Harbor seal	24.5	8.2-56.3	83.8	174.3
Steller sea lion	29.3	8.2-64.2	140.5	204.3
Minke whale	14.5	11.8-17.5	18.3	18.7

[1]The weight of the mean length fish does not correspond to the mean weight of fishes consumed due to the exponential nature of the length-weight relationship for fishes and the distribution of lengths of fishes consumed.

sumed generally agree with the basic distribution pattern for pollock in that sea lions collected near the continental slope ate many large pollock, while ribbon and spotted seals collected north of St. Matthew Island ate almost entirely small pollock. However, concurrent sampling of prey in stomachs and those available in the environment suggest that some selection does occur. Fur seals were found to eat smaller pollock than those caught in otter trawls taken nearby ($\bar{x}$ length = 30.4 cm in seals, 38.3 cm in trawls), while sea lions appeared to select larger fishes ($\bar{x}$ length = 29.9 cm in sea lions, 25.5 cm in trawls) (Loughlin fn. 4). Such comparisons must be interpreted with caution since demersal trawl samples underestimate the abundance of young pollock, most of which occur several meters off the bottom (Traynor[7]).

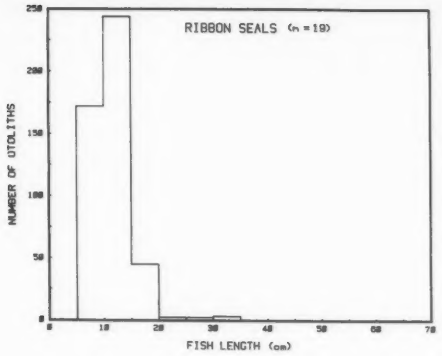
Other information also indicates that marine mammals sometimes select fishes of certain size classes. The sizes of arctic cod, *Boreogadus saida*, caught in otter trawls in the northern Bering Sea were compared with the estimated lengths of fishes eaten by spotted and ribbon seals collected in the same area and time period (Frost and Lowry 1980; Bukhtiyarov et al. 1984). While the distribution of trawl-caught fishes was distinctly bimodal, seals ate predominantly fishes of the larger size classes. Saffron cod, *Eleginus gracilis*, eaten by adult white whales, *Delphinapterus leucas*, in the Kotzebue Sound region of the southern Chukchi Sea were larger than those eaten by younger animals collected at the same location on the same dates (Seaman et al. 1982). We obtained similar results in this study for young versus old sea lions. Pitcher (1981) found that pollock eaten by sea lions were significantly longer ($\bar{x}$ = 29.8 cm) than those eaten by harbor seals ($\bar{x}$ = 19.2 cm; $P < 0.001$) collected in the same general locations in the Gulf of Alaska.

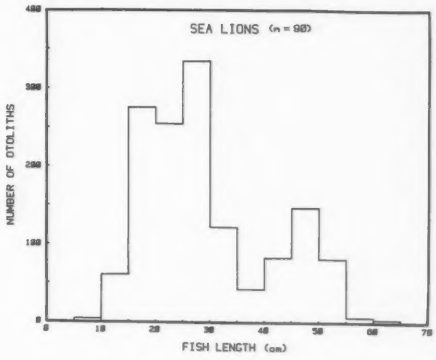
The factors involved in the apparent size selection of prey are poorly known for marine mammals. A strict relationship between the size of predators and the size of their prey is not to be expected in such behaviorally complex and morphologically diverse animals. For example, the prey of ringed seals, *Phoca hispida*, range in length from 1 cm (euphausiids) to at least 121 cm (wolffish, *Anarhichas* sp.) (Frost and Lowry 1981c). The largest animal we examined in this study, a minke whale 7.3 m long, ate uniformly small pollock. Age-related differences in sizes of fishes eaten by sea lions and belukha whales are more likely due to morphological and behavioral development than to size relationships per se. Although size may affect a sea lion's ability to catch large pollock, and old sea lions are larger than young ones ($\bar{x}$ SL = 212 cm for sea lions age 1-4 yr, n = 33 vs. $\bar{x}$ SL = 289 cm for those ⩾5 yr, n = 52), the size range of pollock eaten by both young and old sea lions was similar. The largest pollock (64 cm) represented in our samples was eaten by a 215 cm long, 3-yr-old sea lion which indicates that physical differences due strictly to predator size are not the sole factor influencing preference for a particular prey size. Aspects of feeding strategy, including size selectivity, are the result of a complex and interacting suite of morphological, physiological, and behavioral adaptations which allow an organism to gather food in the most efficient manner (Schoener 1971).

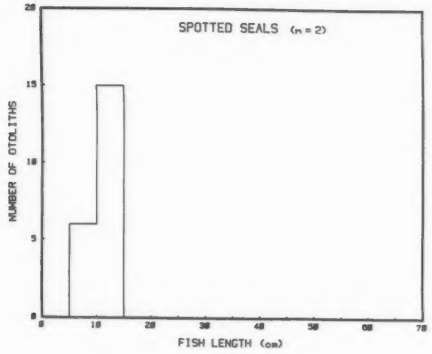
Size-specific feeding may have important consequences for predators. For example, the length of 1-yr-old pollock fluctuates markedly among years, as does the numerical abundance of the first year class. In 1976 abundance was low (729 million individuals in the NMFS Bering Sea survey area) and fishes were small ($\bar{x}$ = 11.6 cm), while in 1974 abundance was high (2,840 million individuals) and fishes were

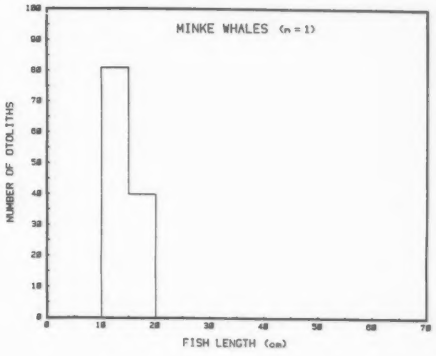
pollock. Unpubl. Rep., 43 p. Northwest and Alaska Fisheries Center, NMFS, NOAA, Seattle, WA.

[7]Traynor, J. J. 1983. Midwater pollock (*Theragra chalcogramma*) abundance estimation in the eastern Bering Sea. Unpubl. Rep., 7 p. Northwest and Alaska Fisheries Center, NMFS, NOAA, Seattle, WA.









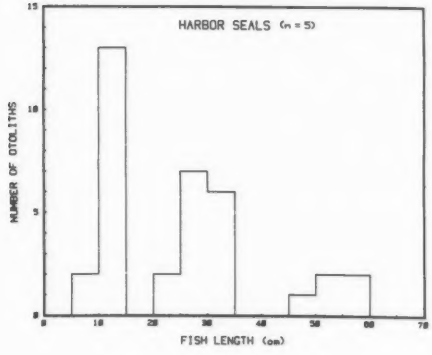


FIGURE 1.—Size distributions of walleye pollock eaten by five species of marine mammals collected in the Bering Sea, 1975-81.

considerably larger ($\bar{x}$ = 15.9 cm) (Smith 1981). The corresponding average individual weights can be estimated as 9.5 and 23.7 g, giving an estimated biomass of age 1 pollock about 10 times greater in 1974 than in 1976. Therefore, the total food available to predators that specialize on small pollock can vary markedly, as can the energy obtained from each fish consumed. Lengths and population sizes of older pollock also vary somewhat among years (Smith 1981); however, predators feeding on large pollock will undoubtedly be exploiting several age classes.

Three species of marine mammals—harbor seals, sea lions, and fur seals—consume age classes of pollock that are also exploited by the commercial fishery (Table 3). A major effect of the pollock fishery has been a reduction in the abundance of older, larger individuals (Pereyra et al.[8]). Major declines in abundance of sea lions and fur seals in the eastern Bering Sea have been reported since the 1950's (Braham et al. 1980; Fowler 1982). Although the evidence is equivocal, especially for the fur seal (see Swartzman and Haar 1983), reduced food availability due to expansion of the pollock fishery has been suggested as a possible cause of the decline in populations. The present population status of other pollock-eating marine mammals in the Bering Sea is not known.

The sizes of fishes consumed by marine mammals are obviously very important for determining the nature and magnitude of marine mammal-fishery interactions. It is particularly important to recognize that because of different feeding strategies, changes in fish stock characteristics caused by fishing may benefit some marine mammal species while having no effect or being detrimental to others.

[8]Pereyra, W. T., J. E. Reeves, and R. G. Bakkala. 1976. Demersal fish and shellfish resources of the eastern Bering Sea in the baseline year 1976. Processed Rep., 619 p. Northwest and Alaska Fisheries Center, NMFS, NOAA, Seattle, WA.

TABLE 3.—Age-class distribution of walleye pollock consumed by marine mammals in the Bering Sea, and caught in the commercial fishery in 1978, based on length-at-age data from Smith (1981).

	Percent of fishes in age class									
Predator species	1	2	3	4	5	6	7	8	9	⩾10
Harbor seal	43	20	23	—	—	3	0	3	3	6
Spotted seal	100	—	—	—	—	—	—	—	—	—
Ribbon seal	98	1	1	—	—	—	—	—	—	—
Steller sea lion	21	40	14	3	5	6	4	2	2	3
Fur seal[1]	49	44	7	—	—	—	—	—	—	—
Minke whale	100	—	—	—	—	—	—	—	—	—
Commercial fishery[2]	2	20	40	18	20	(>5 yr old)				

[1]from McAlister et al. 1976.
[2]from Smith 1981.

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Literature Cited

BAKKALA, R., K. KING, AND W. HIRSCHBERGER.
1981. Commercial use and management of demersal fish. *In* D. W. Hood and J. A. Calder (editors), The eastern Bering Sea shelf: oceanography and resources, Vol. 2, p. 1015-1036. U.S. Dep. Commer., Off. Mar. Pollut. Assessment, NOAA, Rockville, MD.

BRAHAM, H. W., R. D. EVERITT, AND D. J. RUGH.
1980. Northern sea lion population decline in the eastern Aleutian Islands. J. Wildl. Manage. 44:25-33.

BUKHTIYAROV, Y. A., K. J. FROST, AND L. F. LOWRY.
1984. New information on foods of the spotted seal, *Phoca largha*, in the Bering Sea in spring. *In* F. H. Fay and G. A. Fedoseev (editors), Soviet-American cooperative research on marine mammals, Vol. 1 - Pinnipeds, p. 55-59. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 12.

FISCUS, C. H., G. A. BAINES, AND F. WILKE.
1964. Pelagic fur seal investigations, Alaska waters, 1962. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 475, 59 p.

FOWLER, C. W.
1982. Interactions of northern fur seals and commercial fisheries. Trans. N. Am. Wildl. Nat. Resour. Conf. 47:278-292.

FROST, K. J.
1981. Descriptive key to the otoliths of gadid fishes of the Bering, Chukchi, and Beaufort Seas. Arctic 34:55-59.

FROST, K. J., AND L. F. LOWRY.
1980. Feeding of ribbon seals (*Phoca fasciata*) in the Bering Sea in spring. Can. J. Zool. 58:1601-1607.
1981a. Trophic importance of some marine gadids in northern Alaska and their body-otolith size relationships. Fish. Bull., U.S. 79:187-192.
1981b. Foods and trophic relationships of cetaceans in the Bering Sea. *In* D. W. Hood and J. A. Calder (editors), The eastern Bering Sea shelf: oceanography and resources, Vol. 2, p. 825-836. U.S. Dep. Commer., Off. Mar. Pollut. Assessment, NOAA, Rockville, MD.
1981c. Ringed, Baikal, and Caspian Seals. *In* S. H. Ridgway and R. J. Harrison (editors), Handbook of marine mammals, Vol. 2, Seals, p. 29-53. Acad. Press, N.Y.

LOWRY, L. F., AND K. J. FROST.
1981. Feeding and trophic relationships of phocid seals and walruses in the eastern Bering Sea. *In* D. W. Hood and J. A. Calder (editors), The eastern Bering Sea shelf: oceanography and resources, Vol. 2, p. 813-824. U.S. Dep. Commer., Off. Mar. Pollut. Assessment, NOAA, Rockville, MD.
MORROW, J. E.
1979. Preliminary keys to otoliths of some adult fishes of the Gulf of Alaska, Bering Sea, and Beaufort Sea. U.S. Dep. Commer., NOAA Tech. Rep., NMFS Circ. 420, 32 p.
NEMOTO, T.
1959. Food of baleen whales with reference to whale movements. Sci. Rep. Whales Res. Inst. 14:149-291.
PITCHER, K. W.
1981. Prey of the Steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska. Fish. Bull., U.S. 79:467-472.
SCHOENER, T. W.
1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2:369-404.
SEAMAN, G. A., L. F. LOWRY, AND K. J. FROST.
1982. Foods of belukha whales (*Delphinapterus leucas*) in western Alaska. Cetology 44:1-19.
SMITH, G. B.
1981. The biology of walleye pollock. *In* D. W. Hood and J. A. Calder (editors), The eastern Bering Sea shelf: oceanography and resources, Vol. 1, p. 527-551. U.S. Dep. Commer., Off. Mar. Pollut. Assessment, NOAA, Rockville, MD.
SWARTZMAN, G. L., AND R. T. HAAR.
1983. Interactions between fur seal populations and fisheries in the Bering Sea. Fish. Bull., U.S. 81:121-132.

KATHRYN J. FROST
LLOYD F. LOWRY

Alaska Department of Fish and Game
1300 College Road
Fairbanks, AK 99701

OCCURRENCE OF SOME PARASITES AND A COMMENSAL IN THE AMERICAN LOBSTER, *HOMARUS AMERICANUS*, FROM THE MID-ATLANTIC BIGHT[1]

Larvae of the nematode *Ascarophis* sp. were reported by Uzmann (1967b) from American lobsters collected from Hudson, Block, Veatch, and Corsair Canyons on the edge of the continental shelf east and south of southern New England (Fig. 1). Following parasitological examinations of over 3,000 coastal and offshore lobsters, Uzmann (1970) reported that the nematode larvae were restricted almost exclusively to offshore lobsters. Adult *Ascarophis* sp. are intestinal parasites of fishes (Uspenskaya 1953).

Although coastal and offshore lobsters occur off northern and central New Jersey, coastal lobsters are scarce or absent south of Cape May, NJ. There is an active offshore commercial lobster fishery along the edge of the continental shelf south to Norfolk Canyon (Fig. 1).

Materials and Methods

To determine whether offshore lobsters in the Mid-Atlantic Bight have larval *Ascarophis* sp., we examined the guts of 218 American lobsters, *Homarus americanus*, collected from August 1975 through March 1977. Lobsters from this region had not been examined previously for parasites.

One hundred and ninety-seven of the lobsters examined were caught in lobster traps or trawl nets by commercial and research vessels in Norfolk and Washington Canyons and from the shelf and slope between and adjacent to those canyons (areas III-V, Fig. 1) at depths of 73-402 m. The remaining 21 lobsters were caught by trawl nets from research vessels off the coasts of Delaware and New Jersey at depths of 57-95 m (area VIII, Fig. 1).

The intestines and rectum were excised from live lobsters on shipboard (70% of the samples) or in the laboratory at the Virginia Institute of Marine Science, split longitudinally, and fixed in 10% Formalin[2] or in Davidson's fixative. No free parasites were found in the gut contents. In the laboratory, the gut was transferred to 35% glycerine in 70% ethanol, and part of the ethanol evaporated in a 55°C oven. Pieces of the gut were then laid open, pressed between two 35 × 50 mm slides, and examined for the presence of cysts. This procedure followed the recommendation of J. R. Uzmann[3].

Results

Thirty-nine American lobsters were infected with larval *Ascarophis* sp., encapsulated in the anterior wall of the rectum (Table 1). The proportion of infection in 218 lobsters (17.9%) from the Mid-Atlantic Bight was similar to that reported by Uzmann (1967b), when examined in a 2 × 2 contingency table and using Yates' correction for continuity (Elliott 1971). Uzmann (1967b) reported 77 infections in 314 lobsters (24.5%) collected east and south of southern New England. However, Boghen (1978) reported infection in the gills of 82 out of 233 lobsters (35.2%)

[1]Contribution No. 1277, Virginia Institute of Marine Science, Gloucester Point, VA 23062.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3]J. R. Uzmann, Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543, pers. commun. June 1974.

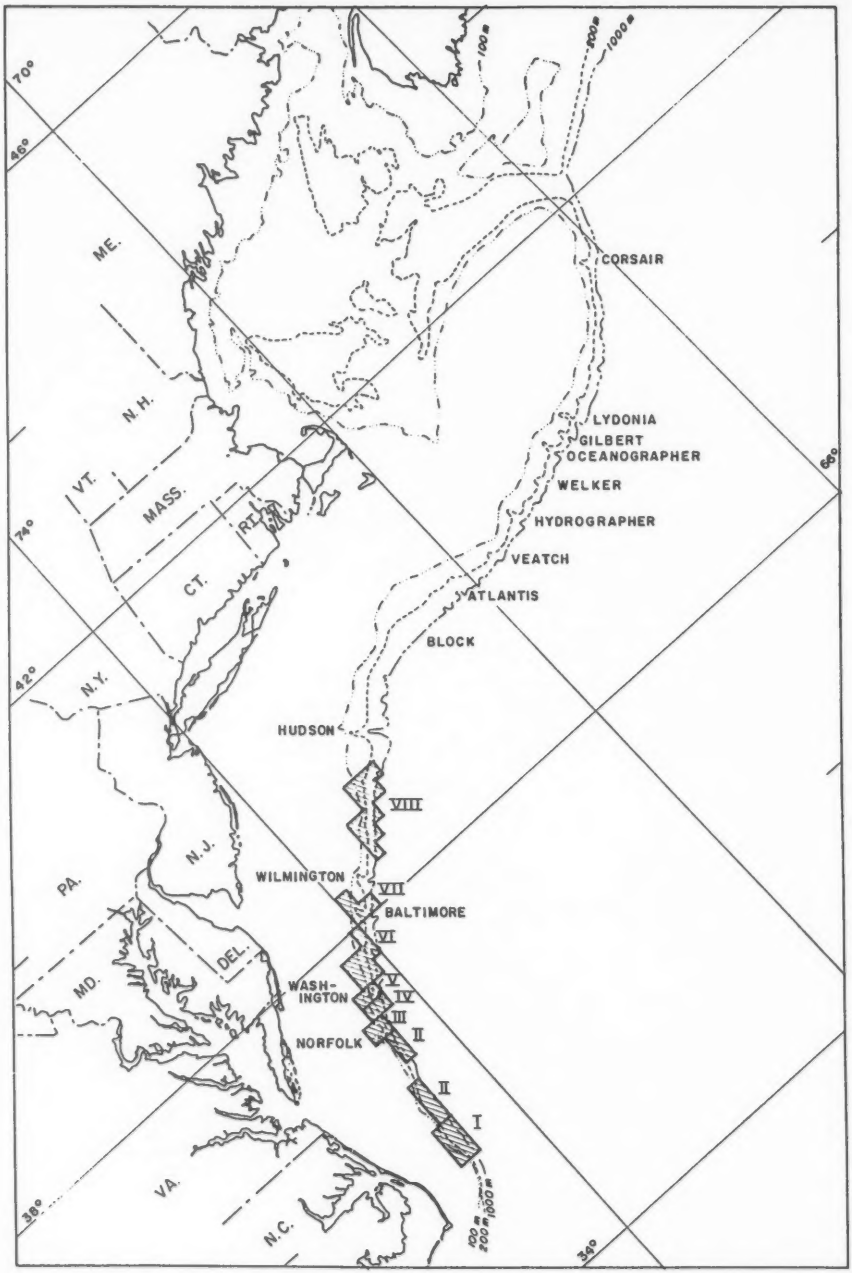

FIGURE 1.—Canyons and lobster sampling sites along the edge of the continental shelf, between Cape Hatteras and the eastern edge of Georges Bank.

TABLE 1.—Prevalence of American lobsters infected with nematodes, *Ascarophis* sp., in the Mid-Atlantic Bight, August 1975-March 1977.

Date	Area[1]	No. lobsters sampled (No. infected) M	F	Sexes combined	Prevalence of infection (%) M	F	Sexes combined
Aug., Sept. 1975	III	26(1)	[2]36(6)	63(7)	3.8	16.2	11.1
Dec. 1975	III	18(3)	18(2)	36(5)	16.7	11.1	13.9
Jan. 1975	III	3(1)	16(5)	19(6)	33.3	31.3	31.6
Jan. 1976	IV	11(1)	13(1)	24(2)	9.1	7.7	8.3
Apr. 1976	III	6(3)	9(2)	15(5)	50.0	22.2	33.3
Apr. 1976	V	4(2)	16(4)	20(6)	50.0	25.0	30.0
July 1976	V	7(1)	5(2)	12(3)	14.3	40.0	25.0
Oct. 1976	V	3(0)	5(2)	8(2)	0.0	40.0	25.0
Nov. 1976	VIII	11(1)	6(2)	17(3)	9.1	33.3	17.6
Mar. 1977	VIII	2(0)	2(0)	4(0)	0.0	0.0	0.0
Total		91(13)	127(26)	218(39)	14.3	20.5	17.9

[1] III. Norfolk Canyon and adjacent slope
IV. Between Norfolk and Washington Canyons
V. Washington Canyon
VIII. Between Wilmington and Hudson Canyons.
[2]One 86 mm female contained 33 acanthocephalan cysts, *Corynosoma* sp.

from Northumberland Strait, southern Gulf of St. Lawrence. That higher proportion of infection was highly significantly different from that reported off southern New England and in the Mid-Atlantic Bight.

Mid-Atlantic Bight lobsters examined for parasites ranged from 49 to 179 mm carapace length (CL) (Table 2). Larval *Ascarophis* sp. were found in 13 (14.3%) of 91 male lobsters and in 26 (20.5%) of 127 female lobsters. No significant difference in prevalence of infection between males and females, when size was ignored, could be demonstrated with a 2 × 2 contingency table analysis. This agrees with the absence of sex specificity in the canyon lobsters

TABLE 2.—Numbers of American lobsters examined and prevalence of infection by the larvae of the nematode *Ascarophis* sp. in the Mid-Atlantic Bight.

Size range, CL mm	No. examined M	F	Sum	No. infected M	F	Sum	Percent of group infected	Percent of total infected	No. larvae, range
40-49	0	2	2	0	2	2	100.0	0.9	1-12
50-59	5	7	12	2	1	3	25.0	1.4	1-9
60-69	9	21	30	1	8	9	30.0	4.1	1-13
70-79	27	29	56	4	7	11	19.6	5.0	1-4
80-89	20	37	57	2	4	6	10.5	2.8	1-5
90-99	16	19	35	3	3	6	17.1	2.8	1-8
100-109	7	8	15	1	1	2	13.3	0.9	2-3
110-119	2	2	4	0	0	0			
120-129	2	1	3	0	0	0			
130-139	0	0	0	0	0	0			
140-149	1	1	2	0	0	0			
150-159	0	0	0	0	0	0			
160-169	1	0	1	0	0	0			
170-179	1	0	1	0	0	0			
Total	91	127	218	13	26	39		17.9	
110-149	5	4	9	0	0	0			
150-179	2	0	2	0	0	0			

reported by Uzmann (1967b) and also reported from Northumberland Strait by Boghen (1978).

Almost one-half (46.3%) of all infections occurred in the 60-79 mm size classes; intensity of infection ranged from 1 to 13 (mean 3.0) (Table 2). None of the 11 lobsters >110 mm CL contained parasites. Boghen (1978) reported 51.3% infection in the 60-69.9 mm range. When the occurrences of parasites in males and females are arranged in three size groups, 40-59, 60-79 and 80-109 mm, and statistically examined with a 2 × 3 contingency table, no departure from the expected 1:1 ratio was observed.

A single specimen of the commensal polychaete, *Histriobdella homari*, was obtained from the gills of a female lobster, 82 mm CL, caught in Norfolk Canyon in June 1974. Gills of four other lobsters were excised, placed in dilute seawater in specimen bowls, and refrigerated overnight. The polychaete was found in the sediment collected from one gill. Because of the small number of lobster gills examined, an estimate of prevalence is inappropriate. Previously, *Histriobdella* was reported by Uzmann (1967a) in the gills and by Simon (1968) in the gills and bodies of New England lobsters, and by Boghen (1978) in the branchial chamber and gills of lobsters from Northumberland Straits.

One female lobster, 86 mm CL, caught in Norfolk Canyon in August 1975, was infected with cysts of an acanthocephalan, *Corynosoma* sp. Thirty-three cysts were found in the intestinal wall and in the mesenteries along the outside of the intestine. Adult *Corynosoma* sp. are parasites of mammals and aquatic birds; crustaceans are first intermediate hosts and fishes are second intermediate hosts (Yamaguti 1963).

According to Uzmann (1970), *Corynosoma* sp. is a discriminator of coastal lobster stocks. Therefore its presence in a lobster taken in Norfolk Canyon indicates that migration from inshore to offshore waters occurs. Montreuil (1954) reported that the acanthocephalan infections in lobsters from the Magdalen Islands, Gulf of St. Lawrence, varied with the sex of the lobster and by season: 20% of females and 20% of males had cysts seemingly acquired towards the end of summer and early fall. Boghen (1978) attributed the absence of cysts in his Northumberland Strait samples to the fact that the lobsters were collected before the end of summer.

Discussion

The variety of animal parasites and their intensity of infection are small in the Mid-Atlantic Bight lobsters. Differences in the occurrence and rates of

infection of *Ascarophis* and *Corynosoma* and of the commensal *Histriobdella* reported from American lobsters of the Mid-Atlantic Bight, southern New England waters, and the Gulf of St. Lawrence, are not large and could be attributed to differences in sample sizes or season of sampling. Peculiarly, cysts of the sporozoan *Porospora* sp. were not seen in Mid-Atlantic Bight lobsters, but occurred in most lobsters in the Gulf of St. Lawrence (Montreuil 1954; Boghen 1978) and were reported by Uzmann (1970) from southern New England waters. Cysts of the trematode *Stichocotyle* sp. were reported by Nickerson (1895) from Penobscot Bay, ME, and from lobster dealers in Boston, MA; by Linton (1940) from an unstated region, probably Woods Hole, MA; by Uzmann (1970) from southern New England waters; and by Montreuil (1954) from southern Nova Scotia or southeastern New Brunswick. Nickerson (1895) found the cysts only in the intestinal tract at the union of the intestine and rectum.

Literature Cited

BOGHEN, A. D.
1978. A parasitological survey of the American lobster *Homarus americanus* from the Northumberland Strait, southern Gulf of St. Lawrence. Can. J. Zool. 56:2460-2462.

ELLIOTT, J. M.
1971. Some methods for the statistical analysis of samples of benthic invertebrates. Freshw. Biol. Assoc., Sci. Pub. 25, 148 p.

LINTON, E.
1940. Trematodes from fishes mainly from the Woods Hole region, Massachusetts. Proc. U.S. Natl. Mus. 88:1-172.

MONTREUIL, P.
1954. Parasitological investigations. Rapp. Ann. Stn. Biol. Mar. Dep. Peches Quebec, Contrib. 50:69-73.

NICKERSON, W. S.
1895. On *Stichocotyle nephropsis* Cunningham, a parasite of the American lobster. Zool. Jahrb., Abt. Anat. Ontog. Tiere 8:447-480.

SIMON, J. L.
1968. Incidence and behavior of *Histriobdella homari* (Annelida: Polychaeta), a commensal of the American lobster. Bioscience 18:35-36.

USPENSKAYA, A. B.
1953. The life cycle of nematodes of the genus *Ascarophis* van Beneden (Nematodes - Spirurata). [In Russ.] Zool. Zh. 32: 828-832. (Translated by J. M. Moulton, Bowdoin College, Brunswick, ME, 1966).

UZMANN, J. R.
1967a. *Histriobdella homari* (Annelida:Polychaeta) in the American lobster, *Homarus americanus*. J. Parasitol. 53: 210-211.
1967b. Juvenile *Ascarophis* (Nematoda:Spiruroidea), in the American lobster, *Homarus americanus*. J. Parasitol. 53: 218.
1970. Use of parasites in indentifying lobster stocks. (Abstr.) *In* Section II, Proceedings of the Second International Congress of Parasitology, p. 349. J. Parasitol. 56(4).

YAMAGUTI, S.
1963. Classification of the Acanthocephala. Systema Helminthum, Vol. V, Acanthocephala. Interscience Publ., 423 p.

W. A. VAN ENGEL
R. E. HARRIS, JR.
D. E. ZWERNER

Virginia Institute of Marine Science
School of Marine Science
College of William and Mary
Gloucester Point, VA 23062

RESILIENCE OF THE FISH ASSEMBLAGE IN NEW ENGLAND TIDEPOOLS[1]

Factors regulating density and species composition of tidepool fishes have been little studied, particularly in comparison to other elements of the intertidal community (Gibson 1982). Twenty-two collections of fishes were made in two tidepools at the Marine Science and Maritime Studies Center of Northeastern University at Nahant, MA, during summers from 1967 to 1985. Initially, the purpose was simply to demonstrate to my summer class in ichthyology the technique of collecting fishes with rotenone. After several years, it became apparent that there would be interest in examing long-term effects of repeated poisoning of the same pools. The purpose of this paper is to report the data from this series of samples and to compare the resilience of this New England tidepool fish fauna with studies done in the Gulf of California (Thomson and Lehner 1976), the central California coast (Grossman 1982), and South Africa (Beckley 1985). Unfortunately, there are no other similar tidepools in the area, so it was not possible to make control collections from unsampled pools.

Methods

The same two tidepools were sampled each summer from 1967 to 1985. The tidepools are located on the ocean side of East Point, in Broad Sound. The higher pool is at about 2 m elevation and is about 1 m deep at high tide; the lower pool is slightly below 1 m elevation, contains extensive red and brown algal growth, and is shallower. Average tidal amplitude is slightly over 3 m. One collection was made each year except for 1969, 1982, and 1983 when two collections were made, spaced about 2 wk apart. Collections

[1]Contribution No. 134 from the Marine Science Institute, Northeastern University, Nahant, MA 01908.

were made with rotenone (about 1 qt Noxfish[2]) at low tide in August, except in 1983 and 1985, when they were made in July and in 1984 when they were made in September. Specimens were taken by dip net from the pools by my students and me. An attempt was made to collect and then count and measure (mm SL) all fishes. Sometimes I used a face mask to find fishes at the bottom of the pool which was closer to the ocean. Many invertebrates also were killed, but no attempt was made to record numbers. The most abundant invertebrates in the 1984 collection were the green crab, *Carcinus maenas* (Linnaeus), and the sea urchin, *Strongylocentrotus droebachiensis* (Müller). Also collected were amphipods, *Gammarellus angulosus* (Rathke), *Calliopius laeviusculus* (Krŏyer), and *Gammarus oceanicus* Segerstrale; isopods, *Idotea baltica* (Pallas); and scale worms, *Harmothoe imbricata* (Linnaeus).

Results

Thirteen species of fishes were collected (Table 1). The number of species per collection varied from 3 to 8 ($\bar{x}$ 5.3). One species, the rock gunnel, *Pholis gunnellus* (Linnaeus), was collected in all 22 samples. Young cunner, *Tautogolabrus adspersus* (Walbaum), were found in all but two collections. The grubby, *Myoxocephalus aenaeus* (Mitchill), and the threespine stickleback, *Gasterosteus aculeatus* Linnaeus, were present in 17 and 15 collections, respectively. The radiated shanny, *Ulvaria subbifurcata* (Storer), was taken 12 times. The seasnail, *Liparis atlanticus* (Jordan and Evermann), was taken in 10 collections, the mummichog, *Fundulus heteroclitus* Linnaeus, in 8. The American eel, *Anguilla rostrata* (LeSueur), was taken four times; young lumpfish, *Cyclpterus lumpus* Linnaeus, three times. Four of the 13 species were taken only once or twice: the Atlantic tomcod, *Microgadus tomcod* (Walbaum); Atlantic silverside, *Menidia menidia* (Linnaeus); ninespine stickleback, *Pungitius pungitius* (Linnaeus); and northern pipefish, *Syngnathus fuscus* Storer. I can detect no long-term change in species composition or number of individuals over the 19-yr period.

The number of specimens per sample varied from 17 to 1,850 ($\bar{x}$ 197.5), but the mean is distorted by the 1,842 young (9-28 mm SL) *Tautogolabrus adspersus* taken in sample 16. Deleting this number, the figures are 17-343 ($\bar{x}$ 119.2). Thus, a "typical" sample would consist of 41 *Pholis gunnellus*, 49 young *Tautogolabrus adspersus*, 12 *Myoxocephalus aenaeus*, 7 *Gasterosteus aculeatus*, and 2 *Fundulus heteroclitus*. One other species might be present, 1 or 2 specimens of any of the other 8 species, most likely *Ulvaria subbifurcata* or *Liparis atlanticus*.

There is great variation from collection to collection in numbers of specimens of the most abundant 4 species: 2-232 *Pholis gunnellus*; 2-1,842 *Tautogolabrus adspersus*; 1-127 *Myoxocephalus aenaeus*; and 1-44 *Gasterosteus aculeatus*. *Ulvaria subbifurcata*, *Liparus atlanticus*, *Cyclopterus lumpus*, and *Fundulus heteroclitus* showed much less variation, 1-12 per collection. The other 5 species were uncommon, numbering 1-4 specimens.

Discussion

To evaluate short-term effects, comparisons can be made between pairs of collections made in 1969, 1982, and 1983 at 2-3 wk intervals. The number of species decreased from 8 to 6 in the 1969 pair and from 7 to 5 in 1982, but the number increased from 3 to 5 in 1983. Four of the 8 species in the first sample in 1969, and 3 of the 7 species in the first sample in 1982, numbered only 1 or 2 specimens, as did one of the species in the second sample of 1983. Numbers of individuals were about the same in the 1969 pair of collections (over 50) and the 1983 pair (74 and 86), but decreased (54 to 17) in the second collection of the 1982 pair. Rapid recolonization of the tidepools clearly takes place. Differences in thoroughness of collecting, plus apparent random variation in the 7 least commonly taken species, can explain the few differences between the paired collections.

Thomson and Lehner (1976) sampled a large tidepool in the Gulf of California 11 times over the period 1966-73. The period of time between sampling ranged from 13 to 78 wk. Number of species ranged from 16 to 26, total 50; number of individuals 435-2,627, total 11,701. No decrease in number of species or individuals over time is apparent from their data (Thomson and Lehner 1970:table 1).

Grossman (1982) sampled a series of rocky tidepools with quinaldine at Dillon Beach in northern California 15 times from January 1979 to May 1981. The period of time between sampling ranged from 4 to 21 wk. Number of species per sample varied from 9 to 18 (excluding the first sample, 12-18), total 29 species; number of individuals was 71-517 per sample [not 520 as in Grossman's (1982) table 3], total 2,853 individuals. The structure of this rocky intertidal fish taxocene was persistent over 29 mo through 15 defaunations (Grossman 1982:table 3).

Beckley (1985) sampled three South African pools

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Abundance and size range (mm SL) of 13 species of fishes collected in two tide

Species	1	2	3	4	5	6	
Pholis gunnellus	11	2 (94-155)	21 (42-162)	20 (40-145)	36 (34-167)	67 (44-160)	(42
Tautogolabrus adspersus	18	2 (77-96)	18 (10-17)	32 (18-30)		28 (11-20)	(9
Myoxocephalus aenaeus	3 (70-105)	4 (61-81)	1 (78)	2 (34-75)	7 (52-67)	20 (53-102)	(36
Gasterosteus aculeatus		3 (34-52)	5 (47-59)		10 (21-59)	2 (54-62)	(12
Ulvaria subbifurcata	2	1 (48)	1		2 (31-71)	1 (20)	
Liparis atlanticus	2		1			3	(23
Fundulus heteroclitus		11 (20-78)	6 (52-65)	"abdt."	4 (22-72)	7 (13-61)	
Anguilla rostrata				2 (60-80)			
Cyclopterus lumpus			1 (15)				(14
Microgadus tomcod				3			
Pungitius pungitius		2 (46-47)					
Menidia menidia							
Syngnathus fuscus							
No. spp.	5	7	8	6	5	7	
No. spec.	36	25	54	51+	59	128	
No. collectors	5	15	8	7	12	8	
Field no.	1231	1250	1359	1367	1531	1534	1
Date	8/16	8/29	8/7	8/21	8/6	8/17	8
Year	1967	1968	1969	1969	1970	1971	1

wo tidepools at Nahant, MA, from 1967 to 1985.

7	8	9	10	11
33 (42-148)	6 (46-138)	8 (41-103)	8 (49-127)	13 (54-141)
48 (9-28)	160 (10-27)	42 (12-28)	6 (11-26)	68 (10-32)
14 (36-92)	2 (69-91)			
42 (12-34)	15 (14-60)	2 (28-59)	3 (49-57)	1 (27)
2 (23-28)				
			6 (38-85)	
	1 (89)			
3 (14-25)				
1 (111)				
7	5	3	4	3
143	184	52	23	82
9	4	8	6	10
1543	1563	1567	1648	1652
8/22	8/17	8/15	8/14	8/19
1972	1973	1974	1975	1976

TABLE 1.—*Continued.*

Species	12	13	14	15	16	17
Pholis gunnellus	12 (49-151)	50 (88-168)	183 (39-170)	57 (44-155)	2 (98-100)	25 (46-144)
Tautogolabrus adspersus	177 (9-65)	56 (11-29)	5 (26-42)	19 (9-24)	1,842 (9-28)	16 (9-23)
Myoxocephalus aenaeus		16 (29-81)	127 (26-72)	20 (17-73)		5 (54-72)
Gasterosteus aculeatus	1 (59)		13 (16-24)	44 (17-58)	6 (23-28)	3 (25-26)
Ulvaria subbifurcata	2 (35-59)	2 (21-79)	12 (20-87)	1 (84)		2 (27-32)
Liparis atlanticus			1 (32)			1 (36)
Fundulus heteroclitus		2 (14-72)				2 (48-74)
Anguilla rostrata			1 (145)			
Cyclopterus lumpus						
Microgadus tomcod		1 (88)				
Pungitius pungitius						
Menidia menidia			1 (78)			
Syngnathus fuscus						
No. spp.	4	6	8	5	3	7
No. spec.	192	127	343	132	1,850	54
No. collectors	7	6	4	9	7	7
Field no.	1657	1663	1752	1760	1769	1774
Date	8/20	8/15	8/16	8/9	8/15	8/17
Year	1977	1978	1979	1980	1981	1982

17	18	19	20	21	22	No. of samples
25	10	52	32	13	232	22
-144)	(100-155)	(30-150)	(49-146)	(38-140)	(35-153)	
16	4	12	46	315		20
-23)	(11-13)	(9-10)	(9-18)	(10-31)		
5	1	10	3	1	23	17
-72)	(92)	(46-71)	(66-75)	(41)	(50-78)	
3					1	15
-26)					(56)	
2	1				7	12
-32)	(80)				(20-96)	
1	1		4	4	11	10
(36)	(38)		(22-27)	(25-28)	17-53)	
2						8
-74)						
			1			4
			(294)			
					9	3
					(10-14)	
						2
						1
						1
						1
7	5	3	5	4	6	13 spp.
54	17	74	86	343	283	4,345 spec.
7	1	10	3	2	7	
774	1775	1777	1780	1801	1802-3	
/17	8/31	7/9	7/27	9/4	7/6	
982	1982	1983	1983	1984	1985	

with rotenone over a 2-yr period at intervals of 1 mo, 3 mo, and 6 mo. She found rapid recolonization but with lower densities of recolonizers in winter than in summer. During 26 monthly samples, only one of the original species did not recolonize the pool, while 13 additional species were found. In Pool 2, which was sampled in 3-mo intervals, 14 species were taken in the initial sample, 7-12 in subsequent samples. Three of the original 14 species failed to recolonize, but 8 additional species were taken. During four repeat visits to Pool 3, the number of species varied between 9 and 14, all but 1 species recolonized the pool, and 5 additional species were recorded.

My study and those of Thomson and Lehner (1976), Grossman (1982), and Beckley (1985) indicate great resilience of species of tidepool fishes in tropical and temperate waters. Recolonization is quite rapid, within a matter of weeks.

Acknowledgments

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Literature Cited

BECKLEY, L. E.
1985. Tidepool fishes: Recolonization after experimental elimination. J. Exper. Mar. Biol. Ecol. 85:287-295.

GIBSON, R. N.
1982. Recent studies on the biology of intertidal fishes. Oceanogr. Mar. Biol. Ann. Rev. 20:363-414.

GROSSMAN, G. D.
1982. Dynamics and organization of a rocky intertidal fish assemblage: the persistence and resilience of taxocene structure. Am. Nat. 119:611-637.

THOMSON, D. A., AND C. E. LEHNER.
1976. Resilience of a rocky intertidal fish community in a physically unstable environment. J. Exper. Mar. Biol. Ecol. 22:1-29.

BRUCE B. COLLETTE

Marine Science and
Maritime Studies Center,
Northeastern University,
Nahant, MA 01908

and

Systematics Laboratory,
National Marine Fisheries Service,
National Museum of Natural History,
Washington, DC 20560

PARASITES OF BENTHIC AMPHIPODS: CILIATES

Benthic gammaridean amphipods were sampled during a 2½-yr period as a part of the Northeast Monitoring Program (NEMP) of the Northeast Fisheries Center, National Marine Fisheries Service. The amphipod survey was designed to determine the kinds of parasites and pathological conditions occurring in amphipod populations that live in and on the sediments of the continental shelf from Maine to North Carolina. Microsporidans of the sampled amphipods have been discussed by Johnson (1985), and this paper presents and discusses data on host distribution, prevalence, effects on the host, and probable relationships, of ciliates parasitizing amphipods from the same samples.

Materials and Methods

Benthic amphipods were collected from 35 stations, mainly on the Georges Bank and Mid-Atlantic Bight (Fig. 1). Amphipods were sampled during 11 cruises, July 1980-November 1982 (Table 1). Each station was sampled from 1 to 10 times during the survey. The 11 stations indicated by solid circles on Figure 1 had the most consistent and numerous populations of amphipods, were sampled at least five times each, and yielded the majority of data presented here. A Smith-McIntyre grab and occasionally an epibenthic sled or scallop dredge were used to obtain the samples. Up to 30 individuals of each species present in a sample, and sometimes more depending on numbers present, were prepared for histological study. Details of collecting procedures and preparation of the amphipods for study are given by Johnson (1985).

Results

Host and geographic distribution of ciliate infection is given in Table 1. Ciliate-infected amphipods were taken in samples from at least one station on every cruise. There was no indication that prevalence was influenced by the season of the year or location of the positive stations. The majority of infected specimens were *Ampelisca agassizi* (Judd), but prevalence of ciliate infection was lower in *A. agassizi* than in the other species found infected (*Pontogeneia inermis* Krøyer, *Phoxocephalus holbolli* Krøyer, *Harpinia propinqua* Sars, and unidentified haustoriids) (Table 2). In three instances, at station 33, cruise G; station 48, cruise I; and station 57, cruise E, individuals of *H. propinqua* or *P. holbolli* were infected

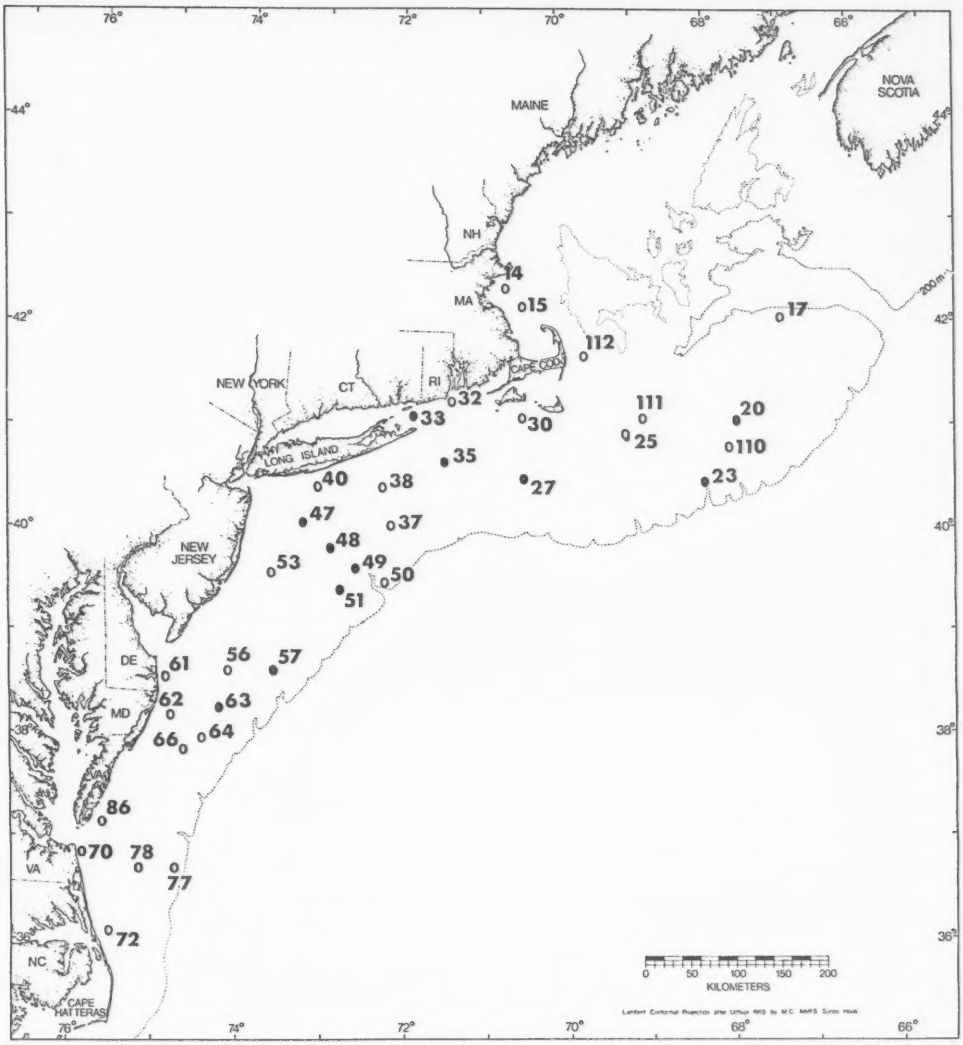

FIGURE 1.—Number designations and positions of Northeast Monitoring Program (NEMP) benthic stations where gammaridean amphipods were sampled during the survey.

but *A. agassizi* collected at the same times were not.

Except for *A. agassizi*, all the species with ciliate infections were rare (Table 2). The most numerous species collected, after *A. agassizi*, were *Leptocheirus pinguis* Stimpson, which made up 11% of the total collected (2,655/24,244), and *Unciola* species (probably all *U. irrorata* Say and *U. inermis* Shoemaker), which made up 10% of the total (2,356/24,244). Despite their abundance, these species were never found infected with ciliates. Considering *all* amphipods sectioned and examined, overall prevalence of ciliate infection was 0.6% (41/7,363).

Light infections consisted mainly of large ciliates. Heavier infections had medium to small ciliates, but

TABLE 1.—Stations with ciliate-infected amphipods, by cruise and host species.

Station	Cruise[1]										
	A	B	C	D	E	F	G	H	I	J	K
20	PI[2]	—[3]	—	—	—	—		—			—
23	AA[2]	AA	AA	—	—	AA		—			—
25		—			PH[2]						
33	—	AA	AA	AA	AA	AA	HP[2]	—	—		
35	—	AA	—	AA	—	—		—		AA	
37				AA							
38			—	—	AA			—			
48			—		AA	—		—	HP		
49	—	—	—	—	—	—			AA		
50				AA							
51	AA	—	—	—	—	—		AA	—		
57	—	—	—	—	AA	PH		—	AA		AA
62	HAU[2]	—			—	—		—			
78		—				—		HAU			

[1]Dates of cruises: A, July 1980; B, Sept. 1980; C, Dec. 1980; D, Apr. 1981; E, July 1981; F, Aug. 1981; G, Nov. 1981; H, Jan. 1982; I, Mar. 1982; J, Aug. 1982; K, Nov. 1982.

[2]Infected amphipods present at the station: PI = *Pontogeneia inermis*; AA = *Ampelisca agassizi*; PH = *Phoxocephalus holbolli*; HP = *Harpinia propinqua*; HAU = unidentified haustoriids.

[3]— = station sampled, no ciliate infections found.

sometimes large forms were also present. The largest ciliates were in the gill of a specimen of *Pontogeneia inermis* (Fig. 2). Measured in paraffin sections, they were about 17 μm × 80 μm. Large forms in other infected amphipods were 16-20 μm × 40-50 μm. The majority of small- and medium-sized ciliates were 17-30 μm in the greater dimension; none were less than 14 μm (Fig. 3). Ciliates were elongate-spindle-shaped, with pointed or sharply rounded ends in *P. inermis*, and oval to subspherical in the other amphipods. The macronucleus of the large ciliates in *P. inermis* was sometimes ribbonlike (Fig. 2), and macronuclei of the smaller ciliates in *P. inermis* and those from the other amphipod species were elongate cylinders or elongate ovals in section (Fig. 3).

None of the infections showed recent evidence of host reaction against the ciliates. The melanized nodules and small hemocytic encapsulations occasionally seen in infected amphipods did not contain recognizable ciliates, and may have been due to other causes.

Few pathological effects were visible in ciliate-infected tissues. Two infected subadult males of *A. agassizi* had karyorrhexis and probable lysis in the transverse abdominal muscles, and one heavily infected female of *A. agassizi*, which had a few early embryos in the brood pouch, also had retained necrotic, mature ova in the ovaries. All infected amphipods had material in the gut, indicating that feeding was continuing. Hemocytes were present in

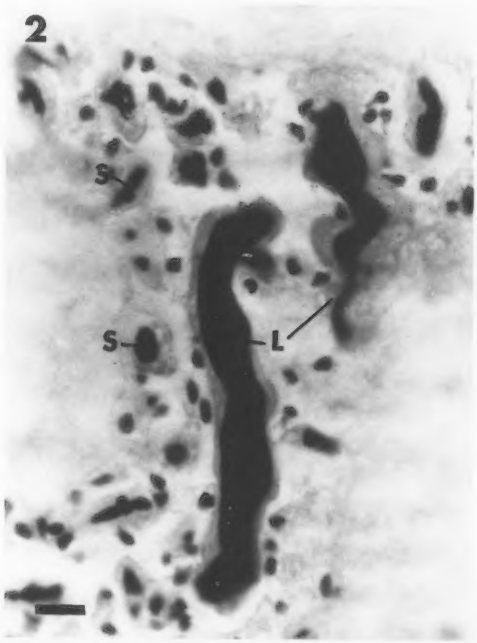

FIGURE 2.—*Pontogeneia inermis*: large and small ciliates in the gill. L, large form; S, small form. Bar = 10 μm.

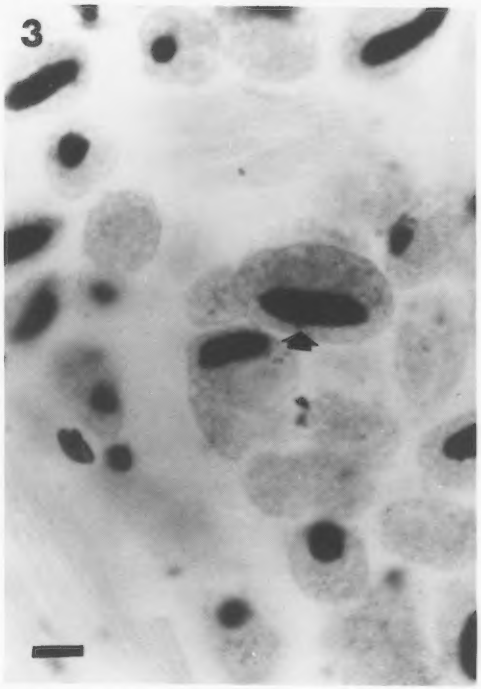

FIGURE 3.—*Ampelisca agassizi*: medium-sized ciliates. The small, pale micronucleus is visible close to the macronucleus in one of the ciliates (arrow). Bar = 10μm.

light to medium infections, but essentially missing in heavy infections. None of the ciliates were positioned in such a way that they appeared to have been phagocytizing hemocytes or other cells at the time of fixation. The granular inclusions commonly present in the cytoplasm of the ciliates bore no resemblance to food vacuoles or phagocytized material.

Discussion

Two groups of ciliates contain species that parasitize crustaceans. *Paranophrys*, in crabs, lobsters, and possibly isopods, and *Parauronema*, in penaeid shrimp, belong in the class Oligohymenophora, order Scuticociliatida (Corliss 1979). They are apparently opportunistic parasites (Bang 1970; Sindermann 1977; Couch 1978; Armstrong et al. 1981; Hibbits and Sparks 1983). The remaining parasites are members of the class Kinetofragminophora, order Apostomatida (Corliss 1979). Typical apostomes are obligate commensals of aquatic crustaceans and have a life cycle geared to their hosts' molting cycles (Bradbury 1966, 1973), but some apostomes have become internal parasites of various invertebrates, including polychaetes, cephalopods, ophiurans, coelenterates, ctenophores, and isopod, amphipod, and decapod crustaceans (Corliss 1979).

Because specialized fixation and staining of whole

TABLE 2.—Species of amphipods infected by ciliates: proportion of the amphipod population and prevalence of ciliate infection.

Species of amphipod	Percent prevalence at positive stations	Proportion of the total amphipods collected
Ampelisca agassizi	3.8% (31/812)	54.3% (13,165/24,244)
Harpinia propinqua	18.2% (2/11)	0.6% (146/24,244)
Haustoriidae spp.	5.4% (3/56)	0.9% (225/24,244)
Phoxocephalus holbolli	9.5% (2/21)	0.5% (125/24,244)
Pontogeneia inermis	10.3% (3/29)	0.7% (164/24,244)

ciliates is necessary for firm identification (Corliss 1979), the amphipod ciliates can be only provisionally assigned to a ciliate group, as is true in other studies based on fixed and embedded material (Sparks et al. 1982; Hibbits and Sparks 1983). On the basis of similarities in hosts and morphology, the amphipod ciliates discussed here are like the apostome genus *Collinia*, whose members parasitize amphipods (Summers and Kidder 1936; de Puytorac and Grain 1975). Like *Collinia*, size of individual ciliates from the benthic amphipods varied greatly and there was no indication that the ciliates were phagocytic. *Paranophrys* and *Parauronema*, on the other hand, belong to a group that ingests particulate material. *Paranophrys* is known to ingest hemocytes and other cells of its hosts, and does not exhibit major size differences (Bang 1970; Sparks et al. 1982; Hibbits and Sparks 1983). Provisionally, the ciliates of benthic amphipods are being considered apostomes.

Whether more than one species of ciliate was involved in the infections is uncertain, but probably the ciliate of *Pontogeneia inermis* represented a species apart from the others. Its very large forms with the ribbonlike macronucleus were not duplicated in other infections.

Although more *A. agassizi* were found infected with ciliates than any other species of amphipod, this was apparently because it was the most abundant and widespread of the susceptible species sampled. *A. agassizi* had the lowest overall prevalence of ciliate infection and sometimes was not parasitized when other species in the same samples were parasitized. There are at least two possible explanations for the odd host distribution of the amphipod ciliates. First, the ciliates might be highly host specific, each amphipod species having its own species of ciliate. Second, the ciliates might be either primary parasites of some other member(s) of the benthic community, or incompletely adapted to a parasitic existence, and thus only occasionally parasitizing the least resistant species of the sampled amphipods. *Unciola* species and *Leptocheirus pinguis* were often the most abundant amphipods at certain stations, but ciliates were never found in individuals of these species, suggesting that they are resistant to ciliate attack. Conversely, the relatively high prevalence of ciliates in the rare species of amphipods could indicate less resistance than is exhibited by most of the species of amphipods sampled.

Presumably, infected amphipods would eventually die of their ciliate infections because of the massive loss of hemocytes. The infrequency of ciliate infection, except in certain rare species, indicates that these parasites are not important in regulating the general amphipod populations they infect.

Acknowledgments

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Literature Cited

ARMSTRONG, D. A., E. M. BURRESON, AND A. K. SPARKS.
1981. A ciliate infection (*Paranophrys* sp.) in laboratory-held Dungeness crabs, *Cancer magister*. J. Invertebr. Pathol. 37:201-209.

BANG, F. B.
1970. Disease mechanisms in crustacean and marine arthropods. *In* S. F. Snieszko (editor), a Symposium on Diseases of Fishes and Shellfishes, p. 383-404. Am. Fish. Soc., Wash., D.C., Spec. Publ. No. 5.

BRADBURY, P. C.
1966. The life cycle and morphology of the apostomatous ciliate, *Hyalophysa chattoni* n.g., n. sp. J. Protozool. 13: 209-225.
1973. The fine structure of the cytostome of the apostomatous ciliate *Hyalophysa chattoni*. J. Protozool. 20:405-414.

CORLISS, J. O.
1979. The ciliated Protozoa. Characterization, classification and guide to the literature. 2d ed. Pergamon Press, Oxford, 455 p.

COUCH, J. A.
1978. Diseases, parasites, and toxic responses of commercial penaeid shrimps of the Gulf of Mexico and South Atlantic coasts of North America. Fish. Bull., U.S. 76:1-44.

DE PUYTORAC, P., AND J. GRAIN.
1975. Etude de la tomitogenèse et de l'ultrastructure de *Collinia orchestiae*, cilié apostome sanguicole, endoparasite du crustacé *Orchestia gammarella* Pallas. Protistologica 11: 61-74.

HIBBITS, J., AND A. K. SPARKS.
1983. Observations on the histopathology caused by a parasitic ciliate (*Paranophrys* sp.?) in the isopod *Gnorimosphaeroma oregonensis*. J. Invertebr. Pathol. 41:51-56.

JOHNSON, P. T.
1985. Parasites of benthic amphipods: microsporidans of *Ampelisca agassizi* (Judd) and some other gammarideans. Fish. Bull., U.S. 83:497-505.

PUYTORAC, P. DE, AND J. GRAIN, See DE PUYTORAC, P., AND J. GRAIN.

SINDERMANN, C. J.
1977. Ciliate disease of lobsters. *In* C. J. Sindermann (editor), Disease diagnosis and control in North American marine aquaculture, p. 181-183. Elsevier Sci. Publ. Co., Amsterdam.

SPARKS, A. K., J. HIBBITS, AND J. C. FEGLEY.
1982. Observations on the histopathology of a systemic ciliate (*Paranophrys* sp.?) disease in the Dungeness crab, *Cancer magister*. J. Invertebr. Pathol. 39:219-228.
SUMMERS, F. M., AND G. W. KIDDER.
1936. Taxonomic and cytological studies on the ciliates associated with the amphipod family Orchestiidae from the Woods Hole district. II. The coelozoic astomatous parasites. Arch. Protistenkd. 86:379-403.

PHYLLIS T. JOHNSON

Northeast Fisheries Center Oxford Laboratory
National Marine Fisheries Service, NOAA
Oxford, MD 21654

FECUNDITY OF THE PACIFIC HAKE, *MERLUCCIUS PRODUCTUS*, SPAWNING IN CANADIAN WATERS

Previous studies on the fecundity of Pacific hake, *Merluccius productus*, have been concentrated on the coastal stock in Baja California (MacGregor 1966, 1971; Ermakov et al. 1974), although large-scale spawning events have been recorded as far north as lat. 38°N, near San Francisco, CA (Stepanenko 1980). The present work was undertaken in conjunction with ichthyoplankton surveys, aimed at estimating the released egg production and spawning biomass of the Pacific hake stock resident in the Strait of Georgia, a semi-closed marine basin in British Columbia (Thomson 1981). The spawning season extends from February through June, peaks in early April, and is 90% complete by mid-May (Mason et al. 1984).

In comparison with the coastal stock of some 1-2 million metric tons (t) (Bailey et al. 1982), this inshore stock, of about 140,000 t, is subject to modest annual exploitation (1-500 t) and resides in a semi-estuarine environment on the known northernmost edge of the reproductive range. The coastal stock undertakes a northward feeding migration after the spring spawning and reaches the southwest coast of Vancouver Island by late summer (Bailey et al. 1982). There is no evidence of intermingling between these two stocks, based on their distributional patterns. The inshore stocks in the Strait of Georgia and Puget Sound may undergo some exchange, possibly due to surface transport of larvae produced in the central Strait of Georgia (Mason et al. 1984). The Puget Sound and coastal stocks have been identified as genetically distinct by Utter and Hodgins (1971), but the two inshore stocks in Puget Sound and the Strait of Georgia have not been similarly compared.

Histological analysis has indicated that only one mode of oocytes developes in Georgia Strait hake. However, like the Baja, California form and hake species elsewhere, some Strait of Georgia hake show evidence of ovarian resorption following spawning (Foucher and Beamish 1980). The quantitative significance of resorption relative to individual and stock fecundities, or to their potential physiological and environmental correlates have not yet been examined. This report considers the "apparent fecundity" as an annual expression of reproductive potential applicable to the stock in the Strait of Georgia, determines that fecundity, and concludes that ovarian resorption is of minor consequence in the stock.

Materials and Methods

The ovaries of 97 Pacific hake females 39-82 cm FL were collected during late February and early March of 1980 and 1981, 71 of which were collected in 1981 (McFarlane et al. 1983). Unspawned females were selected in maturity stages R^2 and R (Foucher and Beamish 1977) when the ovary is yellow and opaque, has prominent blood vessels, and fills one-third to one-half of the coelomic cavity. No ovaries contained translucent oocytes which signify imminent spawning. Fresh ovaries were preserved in 10% formaldehyde solution. In the laboratory, the preserved ovaries were transferred to modified (Simpson 1951) Gilson's fluid for several months to allow breakdown of connective tissue.

Ovaries were then washed thoroughly in cold water over a series of stainless steel screens of 40 μm and larger aperture, and gently broken up by hand when necessary to separate the hardened eggs from the ovarian tissue. The mesh size of the finest screen was determined by the difficulty encountered in separating oocytes <40 μm diameter from ovarian tissue. The cleaned eggs were then stored in 5% formaldehyde solution in preparation for analysis.

Eggs from a single ovary were transferred to a 20 L glass reservoir filled to either 10 or 15 L. While the reservoir was being stirred vigorously with a wooden paddle in a rotating figure-eight pattern, a second worker extracted 50 1-2 mL volumetric subsamples using Stempel pipettes and transferred them to petri dishes. Under the dissecting microscope at 50× magnification, all eggs in five subsamples were sized and counted in 20 μm intervals of oocyte diameter. These results were then combined to construct oocyte size-frequency histograms and

to allot proportions of the combined egg count to the various size intervals. All eggs were counted in the remaining 45 subsamples to provide with the previous 5 subsamples, 50 counts of eggs per unit volume. The total number of eggs in the ovary was calculated from the product of mean subsample count per milliliter and the reservoir volume prior to subsampling. The number of eggs in various size categories was obtained by applying the appropriate proportional value to the estimated total number of eggs in the ovary. Subsample egg counts averaged between 50 and 150 eggs, with the majority falling within 75 and 100. Size-frequency histograms were based on 250-750 sized eggs with the majority based on 375-500 sized eggs. Initial procedural evaluation indicated that 200 sized eggs was sufficient to obtain a replicable size-frequency distribution.

Eighteen ovaries from postspawned females were collected on 3 July 1981 and were similarly processed.

Prespawning females collected in 1981 were aged by the otolith break and burn method (Chilton and Beamish 1982).

Results and Discussion

Frequency Distributions of Oocyte Diameter for Prespawners

Most of the 97 ovaries of prespawners examined contained a pronounced bimodal distribution of oocyte diameters with peaks at about 100 μm and between 500 and 600 μm (Figs. 1-3). Oocytes <150 μm in diameter contained no yolk materials and are taken to constitute a reserve fund for subsequent years (Foucher and Beamish 1980). Oocytes >150 μm diameter were undergoing vitellogenesis, and a few ovaries contained nonhydrated oocytes reaching 700-750 μm diameter. Hydrated eggs were not seen in these ovaries collected in early March and hydration probably does not occur in oocytes <700 μm, although hydrated oocytes from 350 to 950 μm diameter were found by Foucher and Beamish (1980). This apparent discrepancy may reflect their underestimation of oocyte diameters in histological preparations of translucent oocytes due to the plane of sectioning.

The unimodal distribution of yolked oocytes, also reported for *M. m. hubbsi* in the Argentine Sea (Christiansen and Cousseau 1971) does not complement the findings of MacGregor (1966, 1971). He found that ovaries of prespawning coastal hake taken off Baja California contained distinct groups of "small" and "large" yolked oocytes, of which only the latter were destined for release. Furthermore, Ermakov et al. (1974) reported 21% of the 93 female Pacific hake taken off Baja California in 1972 had unimodal, 55% bimodal, 18% trimodal, and 6% quadrimodal oocyte distributions. Similarly, their subsequent sample of 45 ovaries collected in the Oregon-Washington region in late November contained 22% unimodal, 65% bimodal, and 6% trimodal distributions, with major peaks at 200 and 600 μm diameter. Nearly half of the ovaries collected and examined by Ermakov et al. (1974) did not contain a bimodal distribution of yolked oocytes, although these authors concluded that asynchronous development of yolked oocytes indicated the probability of multiple spawnings, most likely two batches within the spawning season.

Estimates of Total Fecundity

Standard errors of mean egg counts for total fecundity estimates of total fecundity (oocytes ≥40 μm diameter) ranged between 0.4 and 4.4% of the means and were <3% in nearly 70% of the 97 ovaries processed. The variability of the enumeration technique compares favorably with that reported by Mason et al. (1983) in an analysis of the fecundity of the sablefish, *Anoplopoma fimbria*, and with that reported by Pitt (1963) on the fecundity of the American plaice, *Hippoglossoides platessoides*, using Wiborg's whorling vessel (Wiborg 1951).

The estimates of total fecundity (oocytes ≥40 μm diameter) increased with fork length according to the equation $F = 0.3081FL^{3.7605}$, [where FL = fork length in centimeters]. The correlation coefficient (r) for the regression was 0.93. An insignificant F ratio from analysis of variance of slope and intercept values allowed pooling of the 1980 and 1981 data.

The smallest and largest Pacific hake females in the sample (39 and 82 cm FL) contained estimated total oocyte complements of 202,100 and 3,009,900 oocytes ≥40 μm, respectively. All 97 fecundity estimates fell within the range of 165,700 and 3,108,000 oocytes ≥40 μm.

Estimates of Fecundity Within Size Classes of Oocytes

The estimated number of oocytes with 20 μm intervals of diameter were summed within five intervals and regressed against fork length to examine the correlation coefficients (Table 1). Coefficients declined progressively with increased oocyte diameter, reflecting increasing variability among

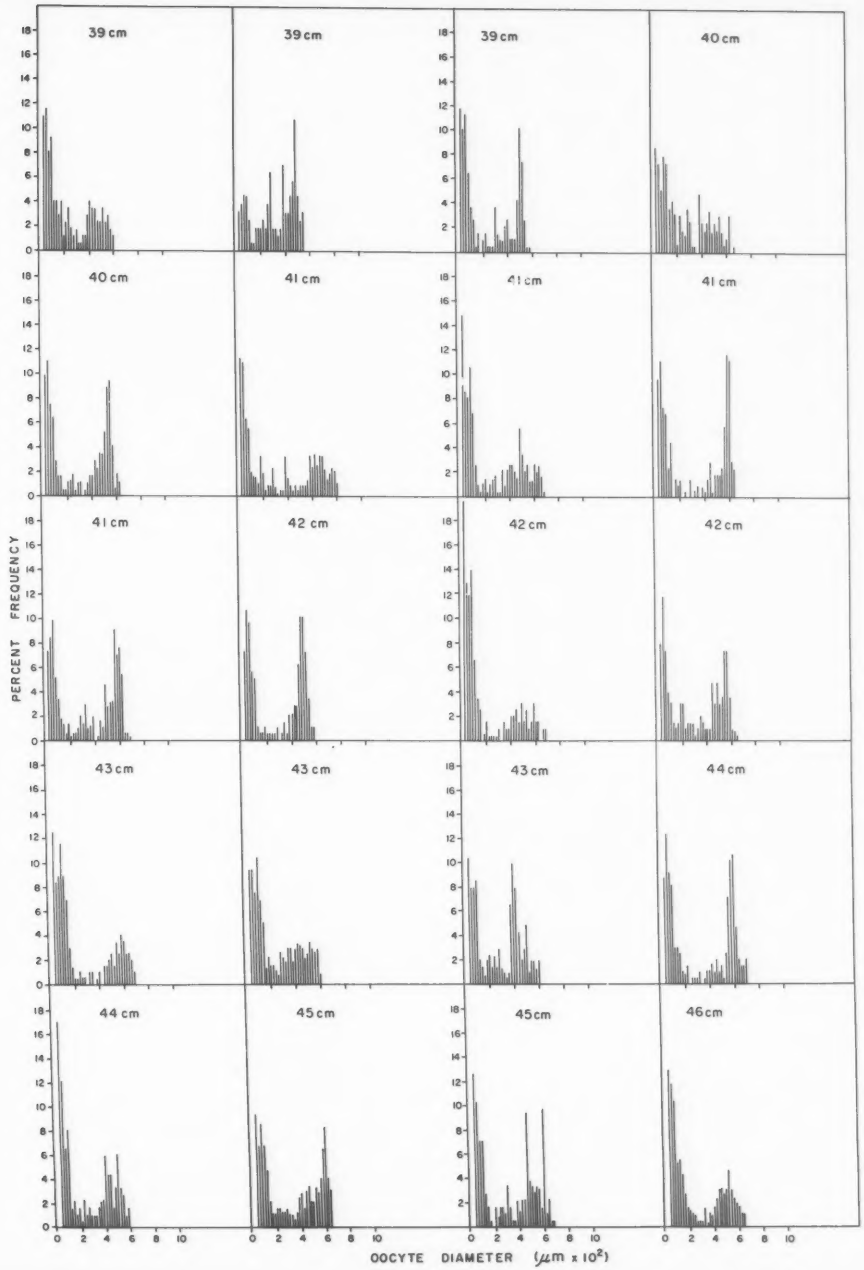

FIGURE 1.—Representative frequency distributions of oocyte diameter from ovaries of Pacific hake 39-46 cm FL.

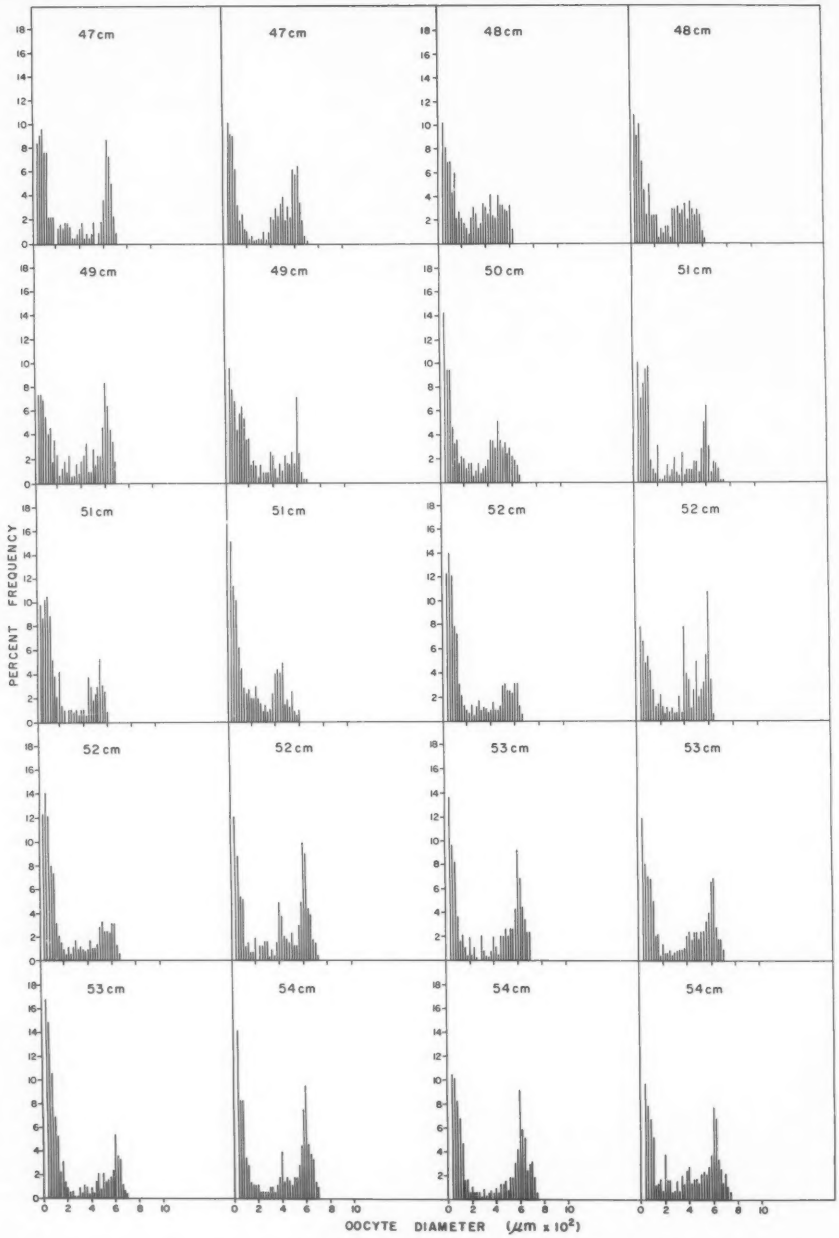

FIGURE 2.—Representative frequency distributions of oocyte diameter from ovaries of Pacific hake 47-54 cm FL.

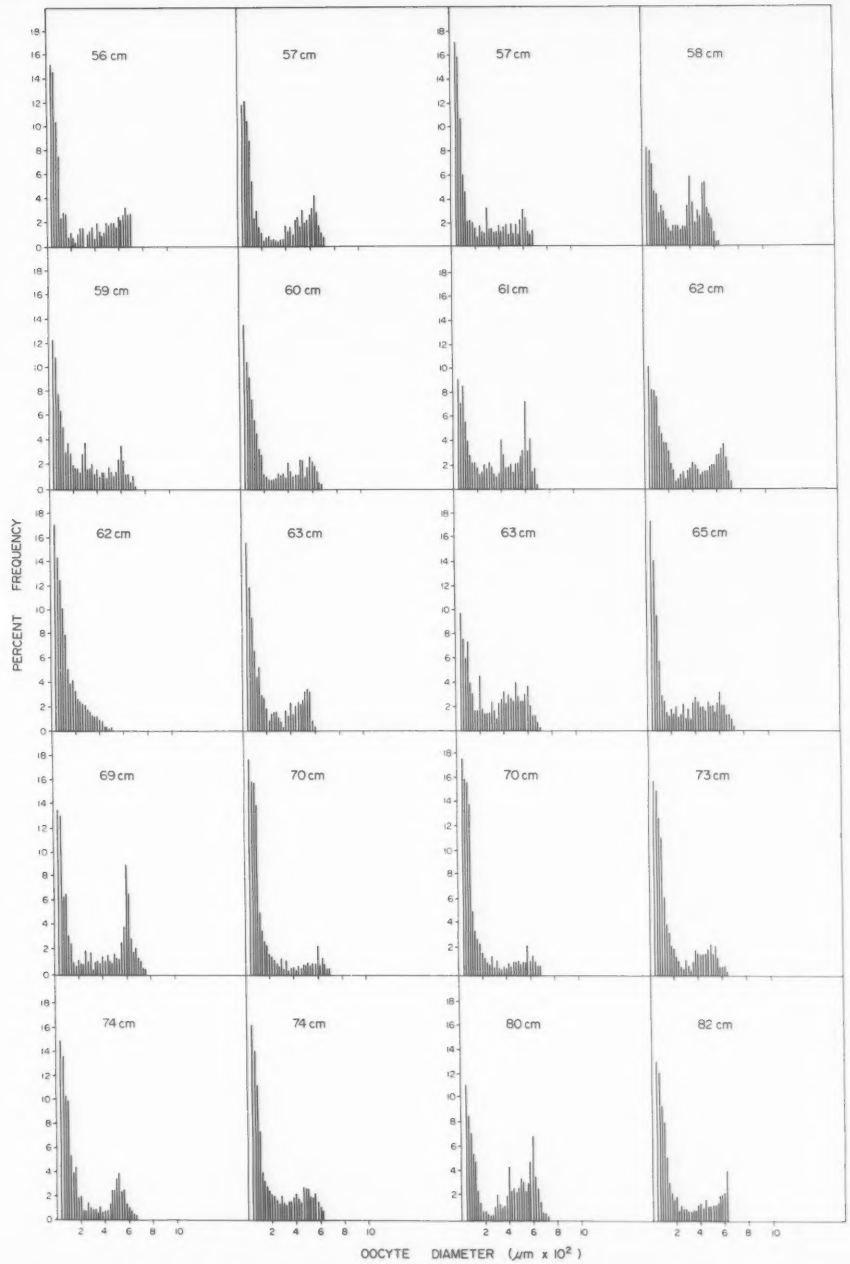

FIGURE 3.—Representative frequency distributions of oocyte diameter from ovaries of Pacific hake 56-82 cm FL.

TABLE 1.—Regression equations for oocytes of several size classes, and some combinations of same, found in prespawned ovaries of Pacific hake from the Strait of Georgia, B.C.

Oocyte diameter (μm)	Oocyte description	Regression equation ($F = aFL^b$)	Correlation coefficient (r)
40-780	all oocytes	$F = 0.3081FL^{3.7605}$	0.93
40-180	unyolked reserve	$F = 0.0692FL^{3.9766}$	0.88
200-380	small, yolked	$F = 0.0446FL^{3.7097}$	0.86
400-580	medium, yolked	$F = 0.2078FL^{3.4174}$	0.71
600-780	large, yolked	$F = 0.0008FL^{4.6370}$	0.65
400-780	medium plus large yolked	$F = 0.1872FL^{3.5640}$	0.75
200-780	all yolked	$F = 0.5501FL^{3.3896}$	0.81

females in the number of maturing oocytes as their maturity stage advanced towards hydration. This may be both a reflection of the range in stage of maturity among individual females at a common time of collection, and variation among females in the proportion of yolked oocytes destined for hydration and release.

Apparent fecundity taken as the number of yolked oocytes ⩾200 μm was best expressed by the equation $F_a = 0.5501FL^{3.3896}$. The averaged female hake in the Strait of Georgia stock (43.3 cm FL) contained an estimated 193,868 yolked oocytes ⩾200 μm and had a relative apparent fecundity of 382.3 eggs/g. In comparison, an uncommonly large female (80 cm FL) could contain more than 1.5 million yolked oocytes for a specific fecundity of 477 oocytes/g (Table 2).

Pacific hake in the Strait of Georgia grow rapidly to age 4, showing almost linear growth in length (McFarlane et al. 1983). Thereafter, growth decreases rapidly and is accompanied by considerable individual variation in annual growth. The largest female in the sample (82 cm FL) was age 18 whereas another female age 15 was only 49 cm FL. Not surprisingly, age was weakly related to apparent fecundity and wide individual differences in apparent fecundity are evident within age classes (Fig. 4).

TABLE 2.—Total and relative (oocytes/g body weight) fecundity estimates at fork length for unyolked (40-180 μm diameter) and yolked (200-780 μm diameter) oocytes found in prespawned ovaries of Pacific hake from the Strait of Georgia, B.C.

Fork length (cm)	Unyolked oocytes		Yolked oocytes		% yolked of unyolked
	Total	Relative	Total	Relative	
40	162,502	406	148,178	370	91.1
45	259,580	455	220,887	388	85.3
50	394,666	507	315,679	403	79.5
55	576,544	551	436,089	417	75.7
60	814,896	598	585,684	430	71.9
65	1,120,308	645	768,233	443	68.7
70	1,504,260	693	987,611	455	65.7
75	1,979,132	739	1,247,812	466	63.1
80	2,558,196	786	1,552,943	477	60.7

Frequency Distributions of Oocyte Diameter in Postspawners

Gonads of 276 adult Pacific hake, trawl-caught on 3 July 1981, were staged superficially for maturity after Foucher and Beamish 1977. All gonads were in postreproductive state. The ovaries of 18 of 111 females retained for microscopic analysis were distributed within the various maturity states with these results: spent (1), recovering (7), and resting (10). Yolked oocytes (200-500 μm) were found in 7 ovaries: spent (1), recovering (4), and resting (2). Number of oocytes ⩾200 μm, expressed as a percentage of the oocytes <200 μm (40-180 μm) was <3% in 6 of these fish, and 11% in the seventh, compared with 85-90% in prespawned ovaries collected in March (Table 2).

These results support previous conclusions that not all yolked oocytes larger than 200 μm diameter are released, as suggested by Foucher and Beamish (1980) and MacGregor (1966). They also suggest that resorbtion in postspawned females probably does not exceed about 5% of the yolked oocytes destined for release.

The female Pacific hake in the Strait of Georgia appears to use progressively less of the reserve fund of unyolked oocytes present during gonadal maturation in subsequent spawnings (Table 2), although relative and apparent fecundity increases with increased fork length. This can be illustrated by comparing females <55 cm FL (Figs. 1, 2) with larger females (Fig. 3). The number of reserve fund oocytes in the size fraction 40-180 μm increases at a faster rate, almost doubling the relative fecundity for reserve fund oocytes in this size fraction by 80 cm FL than does production of larger oocytes. The reserve fund may have several origins, and cytological evidence was presented by Foucher and Beamish (1980) that the fund may be supplemented by cells of follicular origin in the postspawned ovary. Such a mechanism to increase potential fecundity would appear to be rather redundant if significant resorbtion of yolked oocytes commonly occurs.

Stock Differences in Fecundity and Estimates of Spawning Stock

Methodological differences or lack of disclosure, and lack of substantiated assessment of stock-specific resorption following spawning, render it impossible to draw very useful comparisons of fecun-

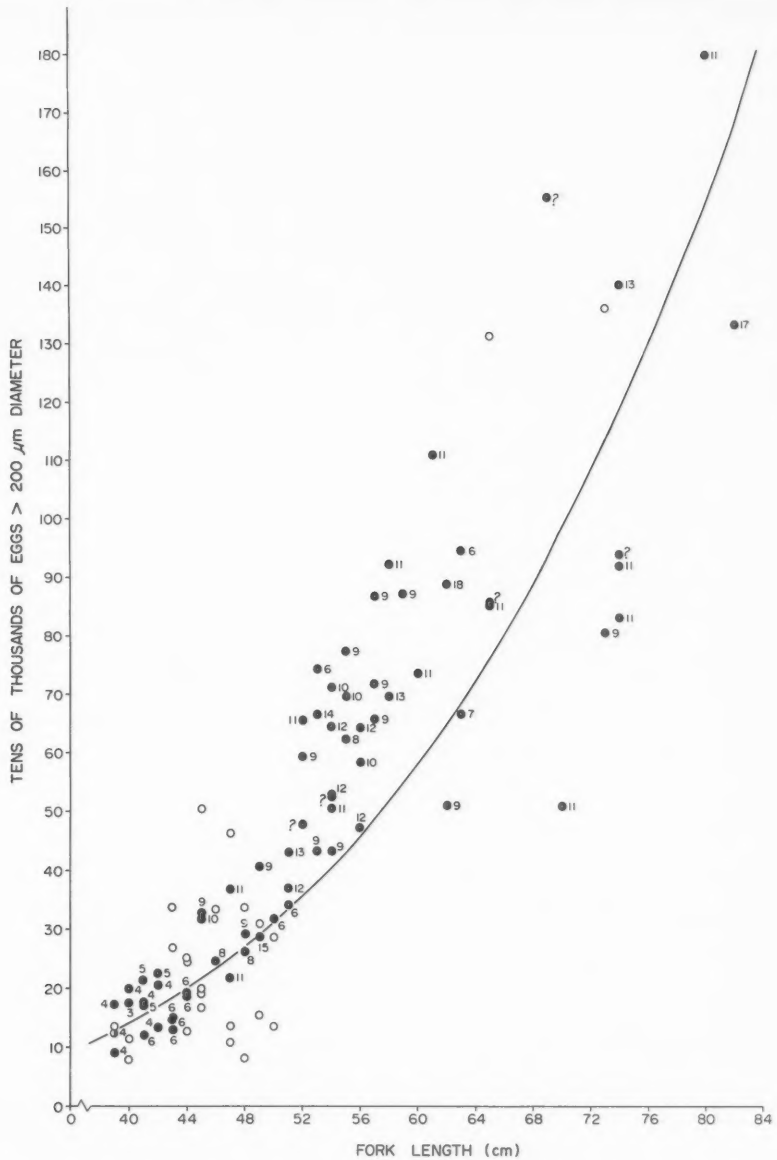

FIGURE 4.—Estimated number of yolked oocytes ≥200 μm diameter in 97 hake ovaries from the Strait of Georgia, B.C., plotted against fork length of female hake. Numbers adjacent to individual plots indicate estimated age of female; open circles - 1980 females, closed circles - 1981 females.

dity between coastal and inshore stocks of Pacific hake at this time. Ermakov et al. (1974) excluded oocytes <100 μm diameter, thus excluding a large fraction of unyolked oocytes constituting the reserve fund. Their estimates of total fecundity (comparable fork length) are one-half to one-third of those reported here for hake in the Strait of Georgia (≥40 mm) and are also lower than the present estimates for apparent fecundity (oocytes ≥200 μm diameter).

MacGregor (1966, 1971) counted advanced, yolked oocytes (>600 μm) only, premised on his assumption that only these cells were destined for release. On the basis of relative fecundity (eggs per gram), for yolked oocytes >580 μm diameter of comparable size to MacGregor's "large, yolked" or "advanced" oocytes, the female Pacific hake in the Strait of Georgia are considerably less fecund (54-164 eggs/g) over the fork length range of 40-80 cm than are Baja California hake which averaged 216 eggs/g (MacGregor 1971). However, the lack of distributional bimodality in the Canadian ovaries renders such a comparison unrealistic, for a common size threshold for resorption, even if appropriate, cannot be applied conveniently to individual ovaries.

We can state with reasonable certainty that resorption of yolked oocytes is a common occurrence in both coastal and inshore stocks of Pacific hake, as has been found in other forms of *Merluccius* (Hickling 1930; Christiansen 1971). The influence of ovarian resorption on annual fecundity of stock and on the magnitude of released egg production from individual females remains unknown. It follows that the application of existing fecundity information to problems of assessing magnitude of Pacific hake spawning stock from released egg production, as determined through ichthyoplankton surveys, should reflect these reservations.

For the Pacific hake stock in the Strait of Georgia, British Columbia, resorption may not involve more than 5-10% of the apparent fecundity. Hence, spawning biomass estimates based on released egg production and the apparent fecundity could be rendered conservative by the observed extent of resorption in this stock.

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Literature Cited

BAILEY, K. M., R. C. FRANCIS, AND P. R. STEVENS.
1982. The life history and fishery of Pacific whiting, *Merluccius productus*. NOAA, NMFS, Proc. Rep. 82-03, NWAFC, Seattle, 81 p.

CHILTON, D. E., AND R. J. BEAMISH.
1982. Age determination for fishes studied by the Groundfish Program at the Pacific Biological Station. Can. Spec. Publ. Fish. Aquat. Sci. 60, 102 p.

CHRISTIANSEN, H. E.
1971. La reproducción de la merluza en el Mar Argentino (*Merlucciidea, Merluccius merluccius hubbsi*). 1. Descripción histologica del ceclo del ovario de merluza (Reproduction of the hake in the Argentine Sea. 1. Histological description of the spawning cycle of the hake). Bol. Inst. Biol. Mar., Mar del Plata 20:1-41. (Engl. transl., Can. Fish. Mar. Serv., Transl. Ser. 4003.)

CHRISTIANSEN, H. E., AND M. B. COUSSEAU.
1971. La reproducción de la merluza en el Mar Argentino (*Merlucciidea, Merluccius merluccius hubbsi*). 2. La reproducción de la merluza y su relación con otros aspectos biológicos de la especie (Reproduction of the hake in the Argentine Sea. 2. Hake reproduction and its relationship with other biological aspects of the species). Bol. Inst. Biol. Mar., Mar del Plata 20:41-73. (Engl. transl., Can. Fish. Mar. Serv., Transl. Ser. 4003.)

ERMAKOV, J. K., V. A. SNYTKO, L. S. KODOLOV, I. I. SEROBABA, L. A. BORETS, AND N. S. FADEEV.
1974. Biological characteristics and conditions of the stocks of Pacific hake, sea perches, sablefishes, and walleye pollock in 1972. Engl. transl., Can. Fish. Mar. Serv. Transl. Ser. 3066, 37 p.

FOUCHER, R. P., AND R. J. BEAMISH.
1977. A review of oocyte development in fishes with special reference to Pacific hake (*Merluccius productus*). Can. Fish. Mar. Serv. Tech. Rep. 755, 16 p.
1980. Production of nonviable oocytes by Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci. 37:41-48.

HICKLING, C. F.
1930. The natural history of the hake. Part III. Seasonal changes in the condition of the hake. Fish. Invest. Minist. Agric. Fish. Food (G.B.), Ser. II, XII(1):1-78.

MCFARLANE, G. A., W. SHAW, AND R. J. BEAMISH.
1983. Observations on the biology of Pacific hake, walleye pollock, and spiny dogfish in the Strait of Georgia, February 20-May 2, and July 3, 1981. Can. MS Rep. Fish. Aquat. Sci. 1722, 109 p.

MACGREGOR, J. S.
1966. Fecundity of the Pacific hake, *Merluccius productus* (Ayres). Calif. Fish Game 52:111-116.
1971. Additional data on the spawning of the hake. Fish. Bull., U.S. 69:581-585.

MASON, J. C., R. J. BEAMISH, AND G. A. MCFARLANE.
1983. Sexual maturity, fecundity, spawning, and early life history of sablefish (*Anoplopoma fimbria*) off the Pacific coast of Canada. Can. J. Fish. Aquat. Sci. 40:2126-2134.

MASON, J. C., A. C. PHILLIPS, AND O. D. KENNEDY.
1984. Estimating the spawning stocks of Pacific hake (*Merluccius productus*) and walleye pollock (*Theragra chalcogramma*) in the Strait of Georgia, B.C. from their released egg production. Can. Tech. Rep. Fish. Aquat. Sci. 1289, 51 p.

PITT, T. K.
1964. Fecundity of the American plaice, *Hippoglossoides platessoides* (Fabr.) from Grand Bank and Newfoundland areas. J. Fish. Res. Board Can. 21:597-612.
SIMPSON, A. C.
1951. The fecundity of the plaice. Fish. Invest. Ministr. Agric. Fish. Food (GB), Ser. II, 17(5):1-27.
STEPANENKO, M. A.
1980. Reproductive conditions and the assessment of the spawning part of the Pacific hake, California anchovy, horse-mackerel, and some other fish species in the California Current Zone in 1979. Pac. Inst. Fish. Oceangr. (TINRO), Manuscr. Rep., 29 p.
THOMSON, R. E.
1981. Oceanography of the British Columbia coast. Can. Spec. Publ. Fish. Aquat. Sci. 56, 219 p.
UTTER, F. M., AND H. O. HODGINS.
1971. Biochemical polymorphisms in the Pacific hake (*Merluccius productus*). Rapp. P.-v. Réun. Cons. int. Explor. Mer 161:87-89.
WIBORG, K. F.
1951. The whirling vessel: An apparatus for the fractioning of plankton samples. Rep. Norw. Fish. Mar. Invest. 9(13): 1-16.

J. C. MASON

Department of Fisheries and Oceans
Fisheries Research Branch
Pacific Biological Station
Nanaimo, British Columbia V9R 5K6, Canada

STRANDED ANIMALS AS INDICATORS OF PREY UTILIZATION BY HARBOR SEALS, *PHOCA VITULINA CONCOLOR*, IN SOUTHERN NEW ENGLAND

Since Federal protection began in 1972, the New England population of harbor seals, *Phoca vitulina concolor*, has more than doubled (Gilbert and Stein 1981[1]; Payne and Schneider 1984), increasing at a site in southeastern Massachusetts at an average rate of 11.9% per year (Payne and Schneider 1984). One of the primary management concerns regarding the New England seal population is the increasing potential for conflict between commercial fisheries and harbor seals (Prescott et al. 1980[2]).

Seals have been shown to be significant consumers of marine production (Brodie and Pasche 1982) and have been implicated as competitors for commercially valuable fish stocks, impacting fisheries through direct predation, gear damage, and entanglement (Boulva and McLaren 1979; Everitt and Beach 1982; Brown and Mate 1983). Despite the significant increase in harbor seal abundance, only anecdotal information exists on the diet of harbor seals along the eastern United States. To assess the impact of this common predator on fish and squid, information is required on the food species exploited.

In the past, seals were killed to facilitate quantitative analysis of their stomach contents (Imler and Sarber 1947; Spalding 1964; Boulva and McLaren 1979; Pitcher 1980a), although this procedure is impractical in New England. Two alternatives to this method are the analysis of the stomachs of stranded animals, and the examination of seal feces collected on accessible haul-out sites (Pitcher 1980b; Treacy and Crawford 1981; Brown and Mate 1983).

The first alternative for determining the food habits of the southern New England seal population was provided by the more than 500 harbor seals that have been found stranded south of Maine since 1977. The stranded seals were collected by the New England Aquarium (NEA), Boston, MA. The majority (59%) of the seals were collected between January and March (Table 1) along the perimeter of Cape Cod Bay, MA, primarily on the eastern side. This corresponds to the time when the peak number of seals occur south of Maine (Schneider and Payne 1983). Most of the stranded seals (65%) came from one year, 1980 (Table 1), when over 445 seals died of acute pneumonia associated with influenza virus (Geraci et al. 1982).

Upon necropsy at the NEA, most of the stomachs and intestinal tracts of the stranded seals were found to be empty. Only 63 stomachs contained food matter, and the contents from those were frozen for later

TABLE 1.—Monthly distribution of stranded *P. v. concolor* containing prey items examined 1977-83.

Month	1977	1978	1979	1980	1981	1982	1983	Total
Jan.	1			15			1	17
Feb.				7	2		1	10
Mar.				10				10
Apr.				1				1
May			1	1	1	2	1	6
June		1				2	1	4
July						1		1
Aug.				2		1	1	4
Sept.				3		2		5
Oct.				1				1
Nov.				1				1
Dec.			2			1		3
Totals	1	1	3	41	3	9	5	63

[1]Gilbert, J. R., and J. L. Stein. 1981. Harbor seal populations and marine mammal fisheries interactions. National Marine Fisheries Service, NOAA, Northeast Fisheries Center, Contract No. NA-80-FA-C-00029, Woods Hole, MA 02345, 55 p.

[2]Prescott, J. H., S. D. Kraus, and J. R. Gilbert. 1980. East Coast/Gulf Coast Cetacean and Pinniped Workshop. Marine Mammal Commission (MMC), Final Report, Contract 79/02. (Available National Technical Information Service, Springfield, VA 22151 as PB80-160104, 142 p.)

examination. In the fall of 1983, we pilot-tested the analysis of stomach contents from stranded seals using those 63 stomach samples as an indicator of prey utilization. The objectives of this study were 1) to identify prey items selected by seals in southern New England and 2) to determine whether stomach contents from stranded animals can provide accurate information on the utilization of most kinds of prey.

Methods

The stomachs were thawed and the contents washed with water through a series of nested sieves (1.80, 1.00, and 0.50 mm^2). Identifiable materials were rough-sorted into fish and fish components, invertebrates and invertebrate components. Intact specimens and cephalopod beaks were preserved in a 70% ethanol-30% glycerin solution. Persistent prey hard parts (primarily otoliths) were removed and stored dry in glass vials.

Otoliths from the stomach samples were identified against a reference collection at the National Marine Fisheries Service, Northeast Fisheries Center (NMFS/NEFC), Woods Hole, MA. Cephalopod beaks were identified against a reference key (Clarke 1962).

To estimate the size of fish taken by harbor seals, otoliths removed from the stomach samples were measured under a dissecting microscope using vernier calipers. Regression equations relating otolith length to fish length (Frost and Lowry 1980; Brown and Mate 1983) were calculated using measurements obtained from the reference collection of fishes collected in the Gulf of Maine, located at the NMFS/NEFC. Fork lengths were estimated for four prey species.

Results

Fifty-three stomachs (84%) held identifiable food items (Table 2). Cephalopod beaks were recovered from 35 stomachs, representing at least 168 individuals and 2 species. Thirty-three stomachs contained beaks from the short-finned squid, *Illex illecebrossus*, with a range of 1-22 beaks per stomach. Beaks of the long-finned squid, *Loligo pealei*, were found in two stomachs, ranging from 4 to 5 beaks per stomach, and accounted for only 5% of the squid recovered. The two species were not found together in any of the stomachs. Twenty-nine stomachs contained squid remains and no other type of prey. Six stomachs contained both squid and fish remains.

Seventeen stomachs contained some fish remains, including intact specimens, copious semidigested flesh, and 121 free otoliths. In total, seven species and five families were represented. Fourteen stomachs held otoliths from only one species of fish, while seven stomachs contained otoliths from more than one fish species.

Four species of Gadidae comprised the majority of all fish species found in the stomachs of the stranded seals. A total of 86 otoliths in six stomachs were recovered. Haddock, *Melanogrammus aeglefinus*, was the most frequently found gadid (45 otoliths in four stomachs) with a maximum of 24 otoliths recovered from a single stomach. Silver hake, *Merluccius bilinearis*, remains were found only slightly less frequently (34 otoliths from three stomachs). Pollock, *Pollachius virens*, otoliths were found in one stomach (five otoliths), and two red hake, *Urophycis chuss*, otoliths of equal length were recovered from one stomach, presumably from a single fish.

Fifteen free otoliths and three intact specimens of American sand lance, *Ammodytes americanus*, were recovered from two stomachs, and three stomachs contained otoliths from members of the flatfish family Pleuronectidae.

Two stomachs contained shells: the Atlantic mussel, *Mytilus edulis*, and the common slipper shell, *Crepidula fornicata*.

The estimated mean fork length for the four gadid prey species ranged from 170 to 340 mm (Table 3). Regressions were not available to estimate the lengths of the sand lance found in the stomachs; however, studies on sand lance in Cape Cod Bay found a mean size of 93 mm SL (Richards 1982).

TABLE 2.—Analysis of stomach contents from stranded harbor seals, *P. v. concolor*, in Southern New England, 1977-83.

Species	Stomach (N = 63) Frequency N	%	Min. no. animals
Cephalopoda:			
Illex illecebrossus	33	58.4	159
Loligo pealei	2	3.7	9
Mytilidae:			
Mytilus edulis	2	3.7	12
Calyptraeidae:			
Crepidula fornicata	2	3.7	10
Clupeidae:			
Clupea harengus	1	1.8	1
Gadidae:			
Melanogrammus aeglefinus	4	5.6	23
Pollachius virens	1	1.8	3
Urophycis chuss	1	1.8	1
Merlucciidae:			
Merluccius bilinearis	3	5.6	17
Ammodytidae:			
Ammodytes americanus	2	3.7	11
Pleuronectidae:			
Pseudopleuronectes americanus	3	5.6	10
Unidentified pisces	11	20.8	

TABLE 3.—Estimated sizes of four fish prey species of harbor seals in Southern New England, based on regression equations relating otolith length (OL) to fish fork length (FL).

Species	Regression equation	r^2	n	Estimated prey size (FL, mm) Range	Mean
Melanogrammus aeglefinus	FL = 3.4(OL) − 9.32	0.97	45	110-310	230
Merluccius bilinearis	FL = 22.4(OL) − 1.44	0.98	34	30-460	170
Pollachius virens	FL = 4.9(OL) − 22.58	0.95	5	160-310	280
Urophycis chuss	FL = 25.0(OL) + 0.63	0.96	2		340

Discussion

Analyzing stomach contents from stranded animals to determine prey preference or selection does yield a partial list of prey species exploited; however, several apparent biases prohibit the realization of accurate quantitative results. Therefore, the utility of this method is questionable.

The limited number of stomachs containing food was likely due to the weakened condition of seals prior to stranding and their inability to obtain food. The stomachs that did contain food all came from stranded animals, and therefore may not reflect on what a healthy seal was feeding. The stranded seals were generally animals with debilitating conditions like lungworm and heartworm, and may not have been able to feed in usual feeding areas, or secure usual prey, and thus were probably less selective about prey items.

For example, the shells found in the two stomachs may represent prey items desirable only to a disease-weakened seal. The size and number of these shells suggest that they were not ingested incidentally. Comparing the stomach contents to a "condition index", such as length vs. girth or blubber thickness, might indicate whether the stranded animals are less selective about prey species than healthy ones.

The abundance of squid beaks found in the stomachs suggests that squid are an important part of the diet of harbor seals along coastal New England; however, our own finding of squid beaks in 56% of 63 stomachs may be inflated. Boulva and McLaren (1979) found squid remains in 20.6% of 279 stomachs examined from eastern Canada, and Pitcher (1980b) similarly found cephalopod beaks in 21.1% of 351 harbar seals collected in the Gulf of Alaska. Seals have been shown to retain, then regurgitate, cephalopod beaks rather than pass them through their digestive tract (Miller 1978[3]; Pitcher 1980b). Retention of squid beaks will tend to overrepresent the utilization of squid as a prey species (Pitcher 1980a). The retention of beaks during a period of fasting prior to death may also account for the large percentage (41%) of stomachs containing squid beaks and no other type of prey remains.

Large fish may be underrepresented if the heads (i.e., otoliths) are not eaten (Boulva and McLaren 1979; Brown and Mate 1983). Pitcher (1980b) suggested that seals often fragment large fish while eating them, usually discarding the head.

Finally, the relationship between the time when prey was eaten and when the stomach was collected may determine what types of prey remains will be recovered (Frost and Lowry 1980; Pitcher 1980a; Brown and Mate 1983). For example, the low number of sand lance otoliths found in the stomachs may not accurately represent the importance of sand lance as a prey species of harbor seals in southern New England because otoliths of the size of the ones recovered are very small and delicate and may not remain for long in the seal stomachs once freed from the skull (Smith and Gaskin 1974).

Thus, using only frequency of occurrence as a measure of prey preference or selection may be misleading by overemphasizing the importance of some species. For example, based on number, cephalopods were the major prey item; however *fewer* otoliths representing fish of *greater* weight may show that fish indeed are more improtant. The full importance of fish or squid in the diet of seals can be accurately described only if quantitative assessments such as weight or volume of food items in the stomachs can be determined (Rae 1973; Frost and Lowry 1980).

In summary, given a large sample of animals the analysis of stomach contents from stranded seals does provide information on the types of prey selected. However, the analysis of stomach contents from stranded seals greatly overemphasizes cephalopod remains while likely underrepresenting most

[3]Miller, L. K. 1978. Energetics of the northern fur seal in relation to climate and food resources of the Bering Sea. Marine Mammal Commission, Final Report, Contract MM5AC025. (Available National Technical Information Service, Springfield, VA 22151 as PB-275 296, 32 p.)

species of fish prey due to an extended period of fasting prior to stranding. We consider comparative frequencies of selected prey to be too biased to be useful in any ranking of prey items. Therefore, this technique of analyzing prey utilization should be considered only if the examination of feces or the stomach contents from seals that were healthy when collected are not possible options.

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Literature Cited

BOULVA, J., AND I. A. MCLAREN.
1979. Biology of the harbor seal, *Phoca vitulina*, in Eastern Canada. Fish. Res. Board Can., Bull. 200:1-24.

BRODIE, P. F., AND A. J. PASCHE.
1982. Density-dependent condition and energetics of marine mammal populations in multispecies fisheries management. *In* M. C. Mercer (editor), Multispecies approaches to fisheries management advice, p. 35-38. Can. Spec. Publ. Fish. Aquat. Sci. 59.

BROWN, R. F., AND B. R. MATE.
1983. Abundance, movements, and feeding habits of harbor seals, *Phoca vitulina*, at Netarts and Tillamook Bays, Oregon. Fish. Bull., U.S. 81:291-301.

CLARKE, M. R.
1962. The identification of cephalopod "beaks" and the relationship between beak size and total body weight. Bull. Br. Mus. (Nat. Hist.), Zool. 8:421-480.

EVERITT, R. D., AND R. J. BEACH.
1982. Marine mammal-fisheries interactions in Oregon and Washington: An overview. *In* K. Sabol (editor), Transactions of the North American Wildlife and Natural Research Conference, p. 265-277. Wildl. Manage. Inst., Wash., DC.

FROST, K. J., AND L. F. LOWRY.
1980. Feeding of ribbon seals (*Phoca fasciata*) in the Bering Sea in Spring. Can. J. Zool. 58:1601-1607.

GERACI, J. R., D. J. ST. AUBIN, I. K. BARKER, R. G. WEBSTER, V. S. HINSHAW, W. J. BEAN, H. L. RUHNKE, J. H. PRESCOTT, G. EARLY, A. S. BAKER, S. MADOFF, AND R. T. SCHOOLEY.
1982. Mass mortality of harbor seals: pneumonia associated with influenza A virus. Science 215:1129-1131.

IMLER, R. H., AND H. R. SARBER.
1947. Harbor seals and sea lions in Alaska. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. 28, 23 p.

PAYNE, P. M., AND D. C. SCHNEIDER.
1984. Yearly changes in abundance of harbor seals at a winter haul-out site in Massachusetts. Fish. Bull., U.S. 82:440-442.

PITCHER, K. W.
1980a. Food of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska. Fish. Bull., U.S. 78:544-549.
1980b. Stomach contents and feces as indicators of harbor seal, *Phoca vitulina*, foods in the Gulf of Alaska. Fish. Bull., U.S. 78:797-798.

RAE, B. B.
1973. Further observations on the food of seals. J. Zool. (Lond.) 169:287-297.

RICHARDS, S. W.
1982. Aspects of the biology of *Ammodytes americanus* from the St. Lawrence River to Chesapeake Bay, 1972-75, including a comparison of the Long Island Sound postlarvae with *Ammodytes dubius*. J. Northwest Atl. Fish. Sci. 3:93-104.

SCHNEIDER, D. C., AND P. M. PAYNE.
1983. Factors affecting haul-out of harbor seals at a site in southeastern Massachusetts. J. Mammal. 64:518-520.

SMITH, G. J. D., AND D. E. GASKIN.
1974. The diet of harbor porpoises (*Phocoena phocoena* (L.)) in coastal waters of eastern Canada, with special reference to the Bay of Fundy. Can. J. Zool. 52:777-782.

SPALDING, D. J.
1964. Comparative feeding habits of the fur seal, sea lion, and harbour seal on the British Columbia coast. Fish. Res. Board Can., Bull. 146, 52 p.

TREACY, S. D., AND T. W. CRAWFORD.
1981. Retrieval of otoliths and statoliths from gastrointestinal contents and scats of marine mammals. J. Wildl. Manage. 45:990-993.

LAWRENCE A. SELZER

Manomet Bird Observatory, Manomet, MA 02345

GREG EARLY
PATRICIA M. FIORELLI

New England Aquarium, Boston, MA 02110

P. MICHAEL PAYNE

Manomet Bird Observatory, Manomet, MA 02345
Present address:
Boston University Marine Program, Woods Hole, MA 02345.

ROBERT PRESCOTT

Massachusetts Audubon Society,
South Wellfleet, MA 02663

SCAVENGER FEEDING BY SUBADULT STRIPED BASS, *MORONE SAXATILIS*, BELOW A LOW-HEAD HYDROELECTRIC DAM[1]

A spawning run of striped bass, *Morone saxatilis*, has not been found in the Connecticut River, but subadults from other rivers were reported in the lower 100 km of the river in the 1930's (Merriman

[1]Contribution No. 84 of the Massachusetts Cooperative Fishery Research Unit, which is supported by the U.S. Fish and Wildlife Service, Massachusetts Division of Fisheries and Wildlife, Massachusetts Division of Marine Fisheries, and the University of Massachusetts.

1941). Subadults enter the river in the spring and summer, often in enough abundance to support a sport fishery in Connecticut (Moss 1960). No striped bass were passed upstream in the two Holyoke Dam fish lifts located at river km 140 from the initial operation in 1955 until 1979, when 103 were lifted. Each year from 1980 to 1984, 110-510 striped bass have used the fish lifts (O'Leary 1985). In 1982, 83.5% of the fish were age II; 16.5% were age III; and none were sexually mature (Warner 1983).

Because the striped bass did not migrate into the river to spawn, they probably entered to feed. The food of striped bass has been extensively studied, but there is no published report about the food of young fish that gather below a hydroelectric dam. We studied the food of the striped bass that were lifted at Holyoke Dam in 1982.

Methods

The stomachs of fish were removed and frozen, and the contents were examined in the laboratory with a dissecting microscope. Stomach contents were classified as small forage fish, body parts of large fish (i.e., fish larger than the striped bass could eat whole), insects, plant material, and empty. Body parts were the scales, bones, flesh, and ovaries of adult alosids (i.e., American shad, *Alosa sapidissima*, and blueback herring, *A. aestivalis*), and pieces of adult sea lamprey, *Petromyzon marinus*. The body parts originated from the following sources: fish that were injured or killed while attempting to pass the dam or to use the fish lifts, American shad that were discarded below the dam by sport fishermen, or turbine-induced injuries or mortalities of fish that passed through the hydropower turbine at the dam (Bell and Kynard 1985).

When possible, small forage fish were identified to species and measured for total length. Insects were identified to order. We compared the frequency of occurrence of the four foods eaten by striped bass that were lifted early (25 May-14 June), when average daily passage of adult alosids in the lifts was about 28,000, with the foods eaten by striped bass that were lifted late (after 21 June), when the average daily lift of alosids was about 3,000.

Results and Discussion

We examined 78 stomachs of striped bass—65 (83%) contained food. Sixty-nine percent of the stomachs with food contained the body parts of large fish (Fig. 1a). Of the stomachs with the body parts of large fish, 93% contained the scales of adult alosids, with many containing over 20 scales; 16% contained the body parts of adult sea lampreys.

Small forage fish were second in the frequency of occurrence at 61%, and insects were third at 21% (Fig. 1a). Elvers of the American eel, *Anguilla rostrata*, (96 mm mean total length, range: 70-125 mm, $N = 24$) dominated the small forage fish category, occurring in 58% of the stomachs that contained forage fish. Elvers, migrating upstream from the ocean, may be delayed and concentrated by Holyoke Dam; perhaps striped bass follow the elvers upriver—both species occur in the fish lifts at the same time. Cyprinids were identified in six of the stomachs with forage fish. All had a 2,4-4,2 tooth formula and were probably spottail shiners, *Notropis hudsonius*, a commonly observed minnow. Insects in stomachs were mayfly nymphs, order Ephemeroptera, but only one or two mayflys were found in any stomach.

There was a significant difference in the frequency of the four food groups in fish collected early and late ($\chi^2 = 12.6$, $P < 0.01$). Fish parts dominated the stomach contents of early-lifted fish, whereas in late-lifted fish 54% contained parts of large fish, but 77% contained small forage fish (Fig. 1b). Fifteen percent of the stomachs of early-lifted fish were empty,

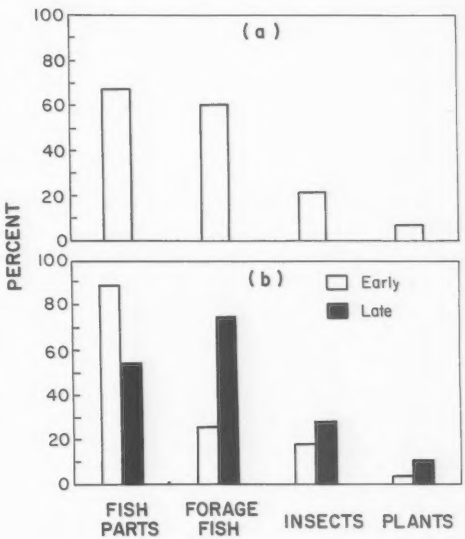

FIGURE 1.—Percent occurrence of the four major foods in the stomachs of striped bass passed by the Holyoke fish lifts a) in all of 1982 and b) in fish sampled early (25 May-14 June, $N = 39$) and late (after 21 June, $N = 26$) 1982.

and 19% of the stomachs of late-lifted fish were empty.

Food of the striped bass at Holyoke Dam was dominated by the body parts of adult American shad, blueback herring, and sea lamprey when many individuals of these species were being lifted, and dominated by forage fish and insects, when the alosids and sea lampreys were scarce (Fig. 1b). The reduced incidence of feeding on the body parts of large fish by striped bass lifted after 21 June was probably the result of a dramatic reduction in the availability of this food that occurred when the run of anadromous alosids diminished.

Hollis (1952) found alosid scales in the stomachs of adult striped bass captured below Conowingo Dam on the Susquehanna River in Maryland, but he dismissed these as accidental. In our study, alosid body parts occurred in stomachs too frequently to be accidental. Many authors consider the food that is selected by striped bass to be directly related to the availability (Hollis 1952; Thomas 1967; Schaefer 1970). During the run of anadromous fish at Holyoke Dam, the most abundant food that is available for striped bass is likely the body parts of dead or injured American shad, blueback herring, and sea lamprey, although we were not able to confirm this by sampling below the dam. About 900,000 adult alosids were passed upstream in the fish lifts in 1982, and injuries and mortalities were commonly observed at the dam and fish lifts. Subadult striped bass may typically concentrate below hydroelectric dams and feed on the parts of fish (anadromous or freshwater species) that die or sustain injury while attempting to move upstream or downstream of the dam.

Acknowledgments

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Literature Cited

Bell, C. E., and B. Kynard.
1985. Mortality of adult American shad passing through a 17-megawatt Kaplan turbine at a low-head hydroelectric dam. North Am. J. Fish. Manage. 5:33-38.

Hollis, E. H.
1952. Variations in the feeding habits of the striped bass, *Roccus saxatilis* (Walbaum), in Chesapeake Bay. Bull. Bingham Oceanogr. Collect., Yale Univ. 14:111-131.

Merriman, D.
1941. Studies on the striped bass (*Roccus saxatilis*) of the Atlantic coast. U.S. Fish Wildl. Serv., Fish. Bull. 50:1-77.

Moss, D. D.
1960. A history of the Connecticut River and its fisheries. Conn. Board Fish. Game, Hartford, 12 p.

O'Leary, J. O.
1985. Connecticut River anadromous fish investigations. Mass. Coop. Fish. Res. Unit, Univ. Mass., D-J Proj. F-45-R-2 Rep., 19 p.

Schaefer, R. H.
1970. Feeding habits of striped bass from the surf waters of Long Island. N.Y. Fish Game J. 17:1-17.

Thomas, J. L.
1967. The diet of juvenile and adult striped bass, *Roccus saxatilis*, in the Sacramento-San Joaquin River system. Calif. Fish Game 53:49-62.

Warner, J. P.
1983. Demography, food habits, and movements of striped bass, *Morone saxatilis* Walbaum, in the Connecticut River, Massachusetts. M.S. Thesis, Univ. Massachusetts, Amherst, 94 p.

John Warner
Boyd Kynard

Massachusetts Cooperative Fishery Research Unit
204 Holdsworth Hall
University of Massachusetts
Amherst, MA 01003

GENETIC CONFIRMATION OF SPECIFIC DISTINCTION OF ARROWTOOTH FLOUNDER, *ATHERESTHES STOMIAS*, AND KAMCHATKA FLOUNDER, *A. EVERMANNI*

The uncertain taxonomic status of two morphological types of *Atheresthes* (family Pleuronectidae) has led to some problems in fisheries surveys and stock assessments. Although data collection would be simplified if these types were conspecific morphs, a single classification would mask differences of distribution and abundance if each type actually represented a distinct species. Each type is described as a separate species: arrowtooth flounder, *A. stomias*, and Kamchatka flounder, *A. evermanni*, based on morphological differences in gill raker count, dorsal and anal fin rays, caudal vertebrae number, eye-dorsal fin distance, and relative position of the upper eye (Norman 1934; Wilimovsky et al. 1967). However, the differences are subtle, and both types have generally been considered *A. stomias* in fisheries surveys (e.g., Smith and Bakkala 1982).

Atheresthes stomias occurs in the eastern Bering Sea and eastern North Pacific Ocean from about St. Matthew Island, southward through the eastern Bering Sea and Gulf of Alaska, and along the North American coast to central California (Hart 1973). *Atheresthes evermanni* is distributed in the western

Bering Sea and western North Pacific Ocean from the Anadyr Gulf, south along the Kamchatka Peninsula, through the Sea of Okhotsk, and to northern Japan (Andriyashev 1939; Wilimovsky et al. 1967). The geographic ranges of the two types overlap in some areas of the Aleutian Islands and eastern Bering Sea.

Biochemical data have recently provided valuable insights towards clarifying genetic relationships among fishes. Findings have ranged from identifying previously unknown species (e.g., Shaklee et al. 1982) to grouping taxa previously considered distinct (e.g., Wishard et al. 1984). Biochemical data were therefore used to clarify the taxonomic status of *A. stomias* and *A. evermanni* through an electrophoretic examination of known individuals of both types. The level of genetic difference observed in this study is compared with that found between two other groups of marine fishes of the Bering Sea and the North Pacific Ocean.

Materials and Methods

Collections were made in the Bering Sea near Unalaska Island by National Marine Fisheries Service research vessels *Oregon* (lat. 53°45′N, long. 166°56′W, August 1980) and *Miller Freeman* (lat. 54°44′N, long. 166°29′W, February 1981). The 12 Kamchatka flounder (4 taken in 1980 and 8 in 1981) included males and females with fork lengths ranging from 24 to 43 cm. The 13 arrowtooth flounder, taken only in 1981, also included both sexes and ranged in fork lengths from 33 to 43 cm. Morphological types were distinguished by the gill raker counts and position of the upper eye. In specimens identified as Kamchatka flounder, the upper eye did not reach the edge of the head and the mean total gill raker count was 12.4. The upper eye of specimens identified as arrowtooth flounder reached the edge of the head, breaking the dorsal profile, and the mean total gill raker count was 15.3. Fish were frozen intact at −20°C following collection and remained frozen up to 30 mo until tissues were removed for electrophoretic analysis.

Sample preparation and electrophoresis followed methods given by Utter et al. (1974). Buffer systems included 1) a discontinuous tris-citric acid (gel pH 8.2), lithium hydroxide-boric acid (tray pH 8.0) buffer, described by Ridgway et al. (1970); 2) a tris-boric acid - 0.004 M EDTA (pH 8.5) buffer, described by Markert and Faulhaber (1965); and 3) an aminopropylmorpholine-citric acid - 0.01 M EDTA (pH 6.5) buffer, described by Clayton and Tretiak (1972).

Procedures of visualizing enzyme activities following electrophoresis were those outlined by May et al. (1979). We followed the criteria of Allendorf and Utter (1979) for the inference of Mendelian inheritance in the absence of breeding data. Genetic data were collected from 22 protein systems (Table 1). A system of nomenclature suggested by Allendorf and Utter (1979) was used where the most common allelic form of a locus was designated as 100, and other allelic forms were assigned values based on their mobility relative to the common form. Alleles migrating cathodally were given negative values.

Phenotypic frequencies of the overall sample (all specimens of both presumed species pooled together) at each polymorphic locus were tested for expected binomial (i.e., Hardy-Weinberg) distributions using a G statistic for goodness of fit (Sokal and Rohlf 1969; Goodenough 1978). Multiple allelic cases were collapsed to two allelic classes to allow for small sample sizes. A contingency table analysis of allelic frequencies testing the null hypothesis of no difference between the two groups also used the G statistic,

TABLE 1.—Protein systems used in this study including tissues and appropriate buffer systems for detection of suitable activity.

Protein system	Enzyme commission number	Tissues[1]	Buffer[2]
Acid phosphatase (ACP)	3.1.3.2	M,L,H	1,2,3
Adenosine deaminase (ADA)	3.5.4.4	M,E	1
Alcohol dehydrogenase (ADH)	1.1.1.1	L	3
Aldolase (ALD)	4.1.2.13	M	1,3
Aspartate aminotransferase (AAT)	2.6.1.1	M	1,2
Creatine kinase (CK)	2.7.3.2	M	1,3
Esterase (EST)	3.1.1.1	L,H,E	3
General protein (GP)		M,E	2,3
Glucosephosphate isomerase (GPI)	5.3.1.9	M,E	1
Glyceraldehydephosphate dehydrogenase (GAP)	1.2.1.12	E,M	1,3
Glycerol-3-phosphate dehydrogenase (G3P)	1.1.1.8	M	3
Glycylleucine peptidase (GL)	3.4.11	E,M	1,2
Isocitrate dehydrogenase (IDH)	1.1.1.42	M,H,E	3
Lactate dehydrogenase (LDH)	1.1.1.27	M,E	3
Leucylglycylglycine peptidase (LGG)	3.4.11	M	1
Malate dehydrogenase (MDH)	1.1.1.37	H,L,E,M	3
Malate dehydrogenase (ME) (decarboxylating - NADP+)	1.1.1.40	M	2
Mannosephosphate isomerase (MPI)	5.3.1.8	M	2
Phosphoglucomutase (PGM)	2.7.5.1	M	1
6-phosphogluconate dehydrogenase (PGD)	1.1.1.44	M,E	3
Phosphoglycerate kinase (PGK)	2.7.2.3	M	3
Superoxide dismutase (SOD)	1.15.1.1	M,H	1,3

[1]M = muscle, L = liver, H = heart, E = eye.
[2]1 = discontinuous tris citrate, lithium borate; 2 = continuous tris, borate, EDTA; 3 = continuous amine citrate, EDTA.

with Yates correction for small sample sizes (Sokal and Rohlf 1969). Nei's (1978) measure of genetic distance for small sample sizes was calculated between the two groups.

Results and Discussions

Data were collected from 22 enzyme systems encoding the following 32 presumed loci (polymorphic loci having one or more variant alleles are indicated by *): AAT*, ACP-1, ACP-2*, ADA*, ADH*, ALD, G3P-1*, G3P-2, CK-1, CK-2, EST, GAP-1*, GAP-2, GL-1, GL-2, IDH*, LDH-1*, LDH-2, LDH-3, LGG*, MDH-1, MDH-2, MDH-3, ME, PGD*, PGM-1, PGM-2, GPI-1, GPI-2*, PGK*, MPI, SOD.

Allelic distributions for the 13 polymorphic loci indicate considerable similarity for most of the systems but some distinct differences as well, based on the contingency analysis (Table 2). The nonsignificant differences observed at nine of the loci are not highly informative given the limited number of individuals that were sampled.

However, the differences that were statistically significant provide considerable information. The most striking difference is at the ADH locus, where no alleles were shared between the 12 arrowtooth and the 10 Kamchatka flounders. These data alone confirm the genetic distinctness of the two types. The allelic distribution between the two forms is almost as distinct at the GAP-1 locus; a lesser, but significant difference also exists at the ACP-2 locus. Gel banding patterns observed for these three loci are shown in Figure 1.

Not surprisingly, the genotypic frequencies at the ADH and GAP-1 loci also deviated significantly ($P < 0.001$) from the ratios of a binomial expansion of allelic frequencies (Hardy-Weinberg equilibrium expected in a single, randomly mating population). This difference resulted from excesses of homozygous and deficits of heterozygous classes, a situation expected in population mixtures (i.e., the Wahlund effect, see Futuyma 1979).

The distinct genotypic distribution of the two forms at the ADH and GAP-1 loci, coupled with their sympatric occurrence and subtle but consistent morphological identities, support their present taxonomic status as distinct congeneric species. However, the value of genetic distance observed, 0.052, is rather low for distinct species suggesting recent speciation (Avise 1976).

Recent genetic studies of two other pleuronectid species sampled from the same geographic region indicate only conspecific variation. The Alaska Peninsula separates two population groups of yellowfin sole, *Limanda aspera*, at a mean genetic distance of 0.005 (Grant et al. 1983). No significant differences of allelic frequencies were detected in Pacific halibut, *Hippoglossus stenolepis*, sampled in the Bering Sea and the North Pacific Ocean (Grant et al. 1984). These various outcomes among confamilial groupings undoubtedly reflect the past and present actions of numerous variables; two major factors are differing capabilities for gene flow based on distinct life history patterns, and differing times and degrees of isolation imposed by glaciation events within the past 2 million years (discussed by Grant and Utter 1984).

Finally, the possibility of hybridization and introgression between the two species of *Atheresthes* should be examined through more extensive sampling of these two forms over a broader geographic range. The distinct distribution of ADH alleles excluded a hybrid origin of any individuals in this study.

TABLE 2.—Observed number and (in parentheses) within group frequency of alleles of 13 polymorphic loci in samples of arrowtooth and Kamchatka flounder.

Locus	Allele	Observed alleles (frequencies) Arrowtooth	Kamchatka	P[1]	Subunit structure[2]
AAT	92	2(0.100)	no data		d
	100	10(0.500)			
	106	8(0.400)			
ACP-2	100	20(0.769)	22(1.000)	<0.05	m
	109	6(0.231)	0(0.000)		
ADA-1	100	24(0.923)	19(0.792)	ns	m
	108	2(0.077)	5(0.208)		
ADH	−100	24(1.000)	0(0.000)	<0.001	d
	−75	0(0.000)	1(0.050)		
	−13	0(0.000)	19(0.950)		
G3P-1	100	24(1.000)	19(0.950)	ns	d
	150	0(0.000)	1(0.050)		
GAP-1	13	0(0.000)	9(0.375)	<0.001	t
	70	0(0.000)	12(0.500)		
	100	26(1.000)	3(0.125)		
GPI-2	100	25(0.962)	24(1.000)	ns	d
	107	1(0.038)	0(0.000)		
IDH	70	0(0.000)	3(0.125)	ns	d
	100	26(1.000)	21(0.875)		
LDH-3	100	26(1.000)	22(0.917)	ns	t
	117	0(0.000)	2(0.083)		
LGG	86	1(0.038)	0(0.000)	ns	d
	100	25(0.962)	22(1.000)		
PGD	75	4(0.154)	0(0.000)	ns	d
	100	22(0.846)	22(1.000)		
PGM-1	84	0(0.000)	1(0.042)	ns	m
	100	23(0.885)	22(0.916)		
	105	3(0.115)	0(0.000)		
	113	0(0.000)	1(0.042)		
PGK	100	26(1.000)	19(0.950)	ns	m
	133	0(0.000)	1(0.050)		

[1]Contingency tests of allelic frequencies using the G-statistic with Yates correction for small sample sizes, assuming all samples drawn from the same population; ns = not significant.

[2]Protein subunit structure based on observed banding patterns of variants; m = monomer, d = dimer, t = tetramer.

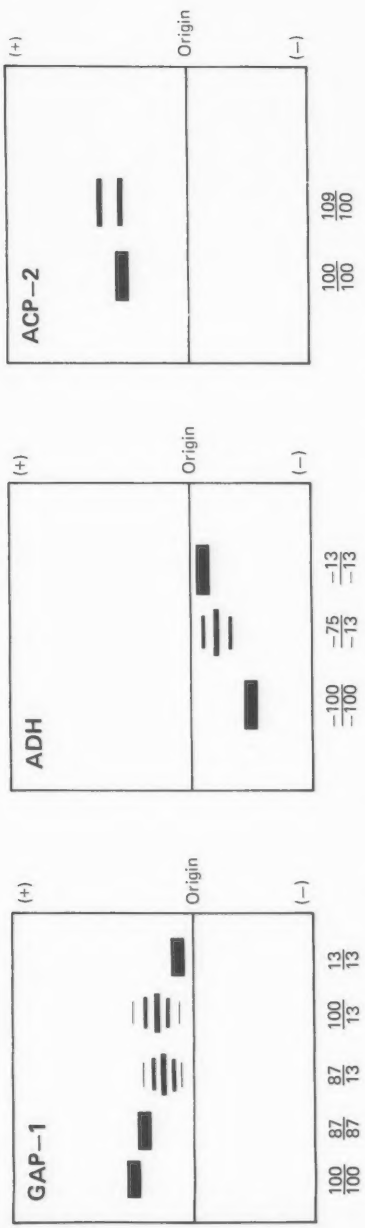

FIGURE 1.—Starch gel banding patterns of variants observed for three loci in *Atheresthes*; GAP-1, ADH, and ACP.

Literature Cited

ALLENDORF, F. W., AND F. M. UTTER.
1979. Population genetics. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (editors), Fish physiology, Vol. 8: bioenergetics and growth, p. 407-454. Acad. Press, N.Y.

ANDRIYASHEV, A. P.
1939. Ocherk zoogeografii i proiskhozhdeniya fauny ryb Beringova morya i sopredel'ynkh vod (Survey of zoogeography and origin of ichthyofauna of the Bering Sea and adjacent waters). [In Russ.] Izd. Leningr. Gos. Univ., Leningr., 187 p. (Transl. Northwest and Alaska Fisheries Center, NMFS, 2725 Montlake Blvd. E., Seattle, WA 98112, 284 p.).

AVISE, J. C.
1976. Genetic differentiation during speciation. *In* F. J. Ayala (editor), Molecular evolution, p. 106-122. Sinauer Assoc. Inc, Sunderland, MA.

CLAYTON, J. W., AND D. N. TRETIAK.
1972. Amine-citrate buffers for pH control in starch gel electrophoresis. J. Fish. Res. Board Can. 29:1169-1172.

FUTUYMA, D. J.
1979. Evolutionary biology. Sinauer Assoc. Inc., Sunderland, MA, 565 p.

GOODENOUGH, U.
1978. Genetics. Holt, Rinehart, and Winston, N.Y., 840 p.

GRANT, W. S., R. BAKKALA, F. M. UTTER, D. J. TEEL, AND T. KOBAYASHI.
1983. Biochemical genetic population structure of yellowfin sole, *Limanda aspera*, of the North Pacific Ocean and Bering Sea. Fish. Bull., U.S. 81:667-677.

GRANT, W. S., AND F. M. UTTER.
1984. Biochemical population genetics of Pacific herring, *Clupea pallasi*. Can. J. Fish. Aquat. Sci. 41:856-864.

GRANT, W. S., D. J. TEEL, T. KOBAYASHI, AND C. SCHMITT.
1984. Biochemical population genetics of Pacific halibut (*Hippoglosses stenolepis*) and comparison with Atlantic halibut (*H. hippoglossus*). Can. J. Fish. Aquat. Sci. 41:1083-1088.

HART, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. 180, 740 p.

MARKERT, C. L., AND I. FAULHABER.
1965. Lactate dehydrogenase isozyme patterns of fish. J. Exp. Zool. 159:319-332.

MAY, B., J. E. WRIGHT, AND M. STONEKING.
1979. Joint segregation of biochemical loci in Salmonidae: Results from experiments with *Salvelinus* and review of the literature on other species. J. Fish. Res. Board Can. 36: 1114-1128.

NEI, M.
1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583-590.

NORMAN, J. R.
1934. A systematic monograph of the flatfishes (Heterosomata). Vol. I. Psettodidae, Bothidae, Pleuronectidae. Br. Mus. (Nat. Hist.), Lond., 459 p. [Reprinted, 1966, by Johnson Reprint, N.Y.]

RIDGWAY, G. J., S. W. SHERBURNE, AND R. D. LEWIS.
1970. Polymorphism in the esterases of Atlantic herring. Trans. Am. Fish. Soc. 99:147-151.

SHAKLEE, J. B., C. S. TAMARU, AND R. S. WAPLES.
1982. Speciation and evolution of marine fishes studied by the electrophoretic analysis of proteins. Pac. Sci. 36:141-157.

SMITH, G. B., AND R. BAKKALA.
1982. Demersal fish resources of the eastern Bering Sea: spring 1976. U.S. Dep. Commer., NOAA Tech. Rep. NMFS

SSRF-754, 129 p.
SOKAL, R. R., AND F. J. ROHLF.
1969. Biometrics. The principles and practice of statistics in biological research. W. H. Freeman, San Franc., 776 p.
UTTER, F. M., H. O. HODGINS, AND F. W. ALLENDORF.
1974. Biochemical genetic studies of fishes: potentialities and limitations. *In* D. C. Malins and J. R. Sargent (editors), Biochemical and biophysical perspectives in marine biology, Vol. 2, p. 213-238. Acad. Press, N.Y.
WILIMOVSKY, N. J., A. PEDEN, AND J. PEPPAR.
1967. Systematics of six demersal fishes of the North Pacific Ocean. Fish. Res. Board Can., Tech. Rep. 34, 95 p.
WISHARD, L. N., J. E. SEEB, F. M. UTTER, AND D. STEFAN.
1984. A genetic investigation of suspected redband trout populations. Copeia 1984:120-132.

CAROL L. RANCK

Northwest and Alaska Fisheries Center
National Marine Fisheries Service, NOAA
2725 Montlake Boulevard East
Seattle, WA 98112
Present address: *Rufus Field Station*
National Marine Fisheries Service, NOAA
P.O. Box 67, Rufus, OR 97050

FRED M. UTTER
GEORGE B. MILNER
GARY B. SMITH

Northwest and Alaska Fisheries Center
National Marine Fisheries Service, NOAA
2725 Montlake Boulevard East
Seattle, WA 98112

ERRATA

Fishery Bulletin: Vol. 83, No. 1

Pérez Farfante, Isabel. "The rock shrimp genus *Sicyonia* (Crustacea: Decapoda: Penaeoidea) in the eastern Pacific," p. 1-79.

Page 4, figure legend was omitted and should be added as follows:

FIGURE 1.—Lateral view of generalized *Sicyonia* showing terms used in description.

Fishery Bulletin: Vol. 83, No. 3

Lester, R. J. G., A. Barnes, and G. Habib. "Parasites of skipjack tuna, *Katsuwonus pelamis*: fishery implications," p. 343-356.

Page 347; Table 2, No. 6, *Syncoelium filiferum*:

J should read 0.2 and K should read 6.9.

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